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Seattle, Washington

U.S. DEPARTMENT OF COMMERCE

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Fishery Bulletin

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A COMPARTMENTALIZED SIMULATION MODEL OF THE SOUTHERN NEW ENGLAND YELLOWTAIL FLOUNDER, *LIMANDA FERRUGINEA*, FISHERY

MICHAEL P. SISSENWINE[1]

ABSTRACT

A compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea*, fishery was developed. The population was divided into 10 age-groups, each of which was subdivided into 7 size categories. The model simulated discard mortality as well as natural mortality and fishing mortality. Fishing and discard mortality rates depended on the level of fishing and on gear and market selection factors. Both linear and density independent stock-recruitment functions were considered. Seasonal variations in growth and exploitation were incorporated into the model. The influence of fluctuation in temperature on recruitment and growth was also simulated. The model using a linear stock-recruitment function accounted for 85.5% of the variability in the yield of the fishery for 1943–65; with a density independent stock-recruitment function, the model explained 83.2% of the variability in yield for the same period.

The linear stock-recruitment model was used to investigate the response of the fishery to alternative fishing strategies. Substantial increases in the past yield of the fishery were indicated by the model when fishing effort was concentrated during the second half of the year and when fishing effort and discard mortality were reduced.

This paper describes a compartmentalized simulation model of the Southern New England yellowtail flounder, *Limanda ferruginea* (Storer), population. There is evidence that production of the Southern New England yellowtail flounder population is influenced by environmental temperature (Sissenwine 1974). The model is intended to demonstrate the feasibility of predicting catch under fluctuating environmental conditions based on the rate of exploitation. The model shares many of the characteristics of Walters' (1969) "generalized computer simulation model," which incorporates growth, fishing and natural mortality, and a stock-recruitment relationship, and also incorporates several additional features. These features include 1) temperature dependent growth and recruitment, 2) growth and fishing mortality rates which vary seasonally, and 3) age-groups subdivided into size categories.

More than 600 thousand metric tons of yellowtail flounder valued at over $120 million have been landed in Southern New England and New York since the onset of fishing in the late 1930's. The magnitude of the fishery has stimulated numerous quantitative investigations. Royce et al. (1959), Lux (1964, 1969a), Brown and Hennemuth,[2] Brown,[3] and Parrack[4] reported catch and fishing effort data for each of the three major fishing grounds (Lux 1963) since 1943. Until recently, most of the catch has been from the Southern New England ground. Catch and fishing effort data were used by Sissenwine (1974) to estimate the annual recruitment and equilibrium catch produced by the Southern New England ground for 1944–65. The equilibrium catch and recruitment were shown to be highly correlated with the atmospheric temperature record at Block Island, R.I. Lux and Nichy (1969) determined the growth rate of the yellowtail flounder. Lux (1969b) and Pitt (1971) calculated the length–weight and length–fecundity functions of the species, respectively. Mortality rates of the yellowtail flounder were estimated by Lux

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[2]Brown, B. E., and R. C. Hennemuth. 1971. Assessment of the yellowtail flounder fishery in Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 71/14, Ser. No. 2599, 57 p.

[3]Brown, B. E. 1972. Current status of the yellowtail flounder fishery in ICNAF Subarea 5 – January, 1972. Int. Comm. Northwest Atl. Fish., Res. Doc. 72/23, Ser. No. 2174, 18 p.

[4]Parrack, M. L. 1973. Current status of the yellowtail flounder fishery in ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 73/104, Ser. No. 3067, 3 p.

(1969a), Brown and Hennemuth (see footnote 2), and Penttila and Brown.[5]

Some of the research cited above is recorded only in unpublished documents. Any information extracted from these reports must be considered as preliminary. Accordingly, the work reported in this paper was primarily based on the published literature.

Catch data used in this paper include both domestic and foreign landings of yellowtail flounder but exclude the industrial catch. All effort data are expressed in standard days fished as defined by Lux (1964).

DESCRIPTION OF THE MODEL STRUCTURE

A diagram representing the compartments and activities of the system is shown in Figure 1. Since yellowtail flounder greater than 10 yr of age are seldom encountered, fish were divided into 10 age-groups. Certainly, the length of individuals within each age-group is not uniform. Therefore, each age-group was subdivided into seven size categories in which all fish were assumed to be of a uniform length. The number of size categories was limited to seven in order to minimize computer cost. The level (number of fish) of each of the 70 age–size compartments is denoted by $N_{i,j}$ where i indicates the age-group and j the size category. Another attribute of each compartment is its mean length, denoted by $L_{i,j}$ with i and j defined in the same manner.

The yield of the fishery in weight (Y_w) and number of fish (Y_n) landed annually are attributes of the yield compartment. Total fecundity of the population during each spawning season is P_e (number of eggs in the egg compartment).

The important activities affecting the system are: 1) fishing which results in a continuous transfer of fish from age–size compartments to the yield compartment and results in some non-productive mortality (discard mortality) since not all fish captured are actually landed (Brown and Hennemuth see footnote 2); 2) natural mortality which results in a continuous decay of each age–size compartment and loss of fish from the system; 3) aging which results in a discrete advancement

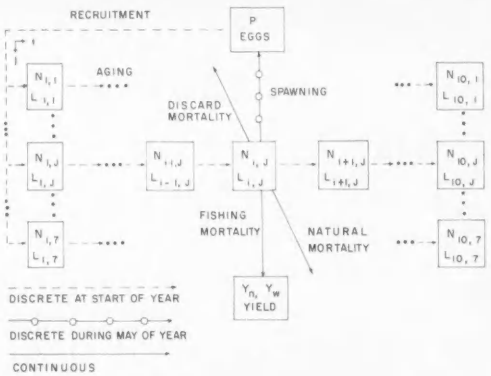

FIGURE 1.—Compartments representing a fish population. Three dots (. . .) indicate additional compartments. The age-group is indicated by i and the size category by j. $N_{i,j}$ is the number of fish in the jth size category of age-group i, and $L_{i,j}$ is the mean length of the fish of the same compartment. Each compartment (only shown for (i,j)) undergoes continuous loss due to fishing, discard, and natural mortality. Losses due to fishing mortality are added to the yield compartment. At the beginning (or end) of each year, aging occurs, advancing each compartment to the next higher age-group, retaining the same value of j. Recruitment to age-group 1 also occurs at the beginning of each year as a function of the previous year's egg production. Spawning occurs during May of each year (only shown for (i,j)) with egg production a function of the number and size of fish in each compartment.

of fish to the next higher age-group (retaining the same value of j) at the beginning of each year; 4) spawning which is the discrete production of eggs (P_e) during May (Bigelow and Schroeder 1953) of each year; 5) recruitment which is represented as the discrete addition of individuals to the youngest age-group of the model at the beginning of each year according to the magnitude of P_e during the previous year; and 6) growth which results in a continuous increase in $L_{i,j}$.

The dynamic system briefly described above was simulated by a FORTRAN program using finite difference approximation. Details of each activity regulating the system are presented below. The variables used in the model are defined in Table 1.

Fishing, Discard, and Natural Mortality

Each age–size compartment is subject to mortality at a rate proportional to the number of fish of the compartment; that is,

[5]Penttila, J. A., and B. E. Brown. 1972. Total mortality rates for two groups of yellowtail flounder estimates from survey cruise data from ICNAF Subarea 5. Int. Comm. Northwest Atl. Fish., Res. Doc. 72/22, Ser. No. 2713, 14 p.

TABLE 1.—List of variables of yellowtail flounder, *Limanda ferruginea*, model.

Variable	Description
$N_{i,j}$	Number of fish in size category j of age-group i
$L_{i,j}$	Length of fish in size category j of age-group i
Y_n	Yield of fishery in number of fish
Y_w	Yield of fishery in weight of fish
P_e	Annual egg production of stock
W	Weight of fish as function of length
Fe	Fecundity of fish as function of length
Z	Instantaneous total mortality rate
D	Instantaneous discard mortality rate
F	Instantaneous fishing mortality rate (excluding discard mortality)
M	Instantaneous natural mortality rate
G	Instantaneous gear mortality rate ($G = F + D$)
f	Instantaneous rate of fishing
t	Time
P_1	Relative gear effectiveness as function of length
P_2	Probability of landing a captured fish as function of length
P_4	Probability of a fish being mature as function of length
T	Index of temperature
k	Growth rate coefficient of von Bertalanffy equation
T_r	Recruitment–temperature factor as function of temperature
T_g	Growth–temperature factor as function of temperature
R	Annual recruitment to age 1

$$\frac{d(N_{i,j})}{dt} = -(F + D + M) \cdot N_{i,j} \qquad (1)$$

where F, D, and M are the instantaneous fishing, discard, and natural mortality rates, respectively, and t is time in years. Total mortality of fish greater than 10 yr old was assumed. Very few fish reach this advanced age. Lux (1964) reported that fish discarded at sea suffered a high mortality rate. In the model, all discarded fish were assumed lost. The yield rate, in number of fish and biomass, contributed by each compartment is

$$\frac{d(Yn)}{dt} = F \cdot N_{i,j} \qquad (2)$$

and

$$\frac{d(Yw)}{dt} = F \cdot N_{i,j} \cdot W(L_{i,j}) \qquad (3)$$

where $W(L)$ is a function relating the weight of a fish to its length. This function assumes the usual form,

$$W(L) = c_1 \cdot L^{c_2}. \qquad (4)$$

The letter c with a numerical subscript is used throughout the paper to denote constants. The total yield rate is obtained by summing $d(Yn)/dt$ and $d(Yw)/dt$ for all age–size compartments.

The mortality rate inflicted by fishermen ($F + D$) on the yellowtail flounder population is assumed to be proportional to the instantaneous annual rate of fishing (f) for fish which are fully vulnerable. This mortality is called the gear mortality (G),

$$G = F + D = q \cdot f \qquad (5)$$

where q is the catchability coefficient. The number of days fished annually is determined externally to the model and acts as a driving variable. Natural mortality was assumed to decrease with age until maturation and then remain constant through the rest of the life span.

In order to approximate the seasonality of fishing, the instantaneous rate of fishing is estimated by multiplying the total number of days fished annually by quarterly effort adjustment factors (c_3, c_4, c_5, and c_6) where the average value of these factors is 1.

Yellowtail flounder first become available to trawl gear on the Southern New England ground in about 1 yr (Brown and Hennemuth see footnote 2), but they are not captured commercially until they have grown to the minimum size retained by the fishermen's nets, L_{gmin}. Some fish continue to escape the nets because of their small size until they have grown to the length at which the gear obtains its maximum effectiveness, L_{gmax}. It is assumed that the relative effectiveness of the gear from fish with a length between L_{gmin} and L_{gmax} can be calculated by linear interpolation. Accordingly, the relative effectiveness of the gear, P_1, is defined as follows:

$$P_1 \begin{cases} (L - L_{gmin})/(L_{gmax} - L_{gmin}) \\ \quad \text{for } L_{gmin} \leq L \leq L_{gmax} \\ 0 \text{ for } L < L_{gmin} \\ 1 \text{ for } L > L_{gmax} \end{cases} \qquad (6)$$

where L is the length for which P_1 is applied.

Since not all of the fish captured are large enough to be marketed (for economic and technological reasons), the probability of landing a captured fish (P_2) as a function of its length must be calculated. Let L_{mmin} be the minimum length landed by the fishermen and L_{mmax} be the length at which all fish are landed. Note that the determination of the marketability of each fish is made by the fishermen on the decks of their vessels. Therefore, a gradual transition from total unacceptability to total acceptability as L increases is expected. Again applying linear interpolation,

$$P_2 \begin{cases} (L - L_{m\min})/(L_{m\max} - L_{m\min}) \\ \quad \text{for } L_{m\min} \leq L \leq L_{m\max} \\ 0 \text{ for } L < L_{m\min} \\ 1 \text{ for } L > L_{m\max}. \end{cases} \quad (7)$$

Using Equations (5), (6), and (7); G, F, and D are calculated as follows for fish of any length:

$$G = q \cdot f \cdot P_1 \quad (8)$$
$$F = q \cdot f \cdot P_1 \cdot P_2 \quad (9)$$
$$D = q \cdot f \cdot P_1 \cdot (1 - P_2). \quad (10)$$

Since G, F, and D vary with L and f, they are time dependent functions.

Aging

The aging process of yellowtail flounder is simulated by advancing individuals of each age–size compartment to the next higher age-group within the same size category.

Growth

The mechanism used in the model to simulate growth was based on the von Bertalanffy growth function. The von Bertalanffy function can be expressed in many forms, but the following is most applicable to this study:

$$L = L_m + (L_0 - L_m) \cdot e^{-kt} \quad (11)$$

where L_m is the maximum length obtained by the fish of the population, L_0 is the length of a fish at the beginning of a time interval of duration t, k is the growth rate coefficient that applies during the interval, and L is the length obtained by the end of the interval. The derivative of Equation (11) is identical to the growth equation deduced by von Bertalanffy (1938).

A single value of L_m is usually assumed for an entire population. In the model, differences in the mean length of size categories are maintained by assigning a unique maximum value to L for each size category ($L_{m1}, L_{m2}, \ldots, L_{m7}$). Fish are distributed among the size categories in the following manner. Assume L_m is a normally distributed random variable with mean L_{m4} and standard deviation s_m. For $G_1, G_2, \ldots, G_7$, the portion of the population in each size category respectively (in the absence of fishing), the range of values of L_m included in each size category can be determined from a standard normal table. The mean value of L_m for the jth size category (L_{mj}) is obtained by integrating the product of the normal density function and the random variable L_m over the range of values of L_m included in the size category and then dividing the result by G_j.

Taylor (1962) showed that k of the von Bertalanffy function was related to water temperature for a number of species, and there is evidence (which is discussed later in this paper) that this is also true for the Southern New England yellowtail flounder. The influence of temperature on k is simulated by adjusting k by a multiplicative growth–temperature factor, T_g, defined as

$$T_g = 1 + c_{14} \cdot (T - \bar{T}) \quad (12)$$

where T is an index of temperature and $\bar{T}$ is the average value of the index over the total period for which data are available. T is an exogenous variable of the model.

Different values of k (k_1, k_2) were necessary to describe the growth of yellowtail flounder less than and greater than 2 yr old (Lux and Nichy 1969). Seasonal variations of growth were incorporated into the model by multiplicative quarterly growth factors K_1, K_2, K_3, K_4 (with an average value of 1.0). The length of age–size compartment i,j after an interval of time t is calculated according to Equation (11) using the length of the compartment at the beginning of the interval L_{mj}, and k as follows:

$$k = k_a \cdot k_n \cdot T_g \quad (13)$$

where n indicates the quarter of the year and a indicates age less than or greater than 2 yr.

Spawning

Spawning occurs during May or at 0.4 of each year. The fecundity–length function of the yellowtail flounder was assumed to be of the usual form,

$$Fe(L) = c_7 \cdot L^{c_8} \quad (14)$$

where Fe is the egg production of a mature female fish of length L. Not all fish mature at the same age or length. Royce et al. (1959) found that maturation was more closely associated with length than age. A relationship of the following form, expressing the probability of a fish of specific length being mature (P_4) was assumed.

$$P_4 = \begin{cases} y_3 \text{ for } 0 \leq P_3 = c_9 + c_{10}L \leq 1 \\ 0 \text{ for } P_3 < 0 \\ 1 \text{ for } P_3 > 1. \end{cases} \quad (15)$$

Equation (15) assumes maturation is a linear function of length in the transition zone between the length below which the entire population is immature and the length above which the entire population is mature. Assuming that the proportion of females in the population is constant, c_{11}, then the egg production of each age–size compartment is the product of $N_{i,j}$, $Fe\,(L_{i,j})$, P_4, and c_{11}. The total egg production of the population (P_e) is obtained by summing over all age–size compartments.

Recruitment

The possibilities that recruitment is a linear function of egg production and that recruitment is independent of egg production, under average environmental conditions, were considered. There is evidence (Sissenwine 1974) that recruitment of the Southern New England yellowtail flounder is also related to temperature. In fact, most of the variability in estimated recruitment for 1944–65 was explained by anomalies in air temperature, ignoring egg production. In order to simulate the influence of temperature, a recruitment temperature factor (T_r) was defined as follows:

$$T_r = 1 + c_{12} \cdot (T - \bar{T}). \quad (16)$$

The number of recruitments as affected by temperature is calculated by multiplying the level of recruitment expected at average temperature conditions by T_r.

The total recruitment (R) of a year class (at age 1) is calculated by

$$R = c_{13} \cdot P_e \cdot T_r \quad (17)$$

or

$$R = c_{13} \cdot T_r. \quad (18)$$

The parameter c_{13} has a different value in each equation. Equation (17) is applicable when recruitment is linearly related to P_e for average temperature conditions. Equation (18) is applicable when recruitment is independent of P_e. Equations (17) and (18) will be referred to as the linear and density independent recruitment functions, respectively. The model described in this paper incorporating either Equation (17) or (18) will be referred to as the linear or density independent models, respectively. Recruits are assigned to size categories of age-group 1 by multiplying R by the appropriate value of G_j.

Parameter Estimation

Estimates of the parameters of the model were taken from the literature or based on published or unpublished data sources. The parameter values used in all the simulations reported in this paper (unless otherwise stated) are shown in Table 2 along with citations of the source of the estimate. Special attention is given below to the estimation of some parameters and initial conditions. These estimates of parameters and initial conditions required some subjectivity.

The natural mortality rate of the yellowtail flounder has yet to be precisely estimated. Lux (1969a) estimated that the upper limit on natural mortality of adult yellowtail flounder is 0.20. Beverton and Holt (1957) estimated the natural mortality of a similar species (North Sea plaice) as 0.10. Values of instantaneous natural mortality of 0.10 and 0.20 have been used in the literature in the past. An instantaneous natural mortality rate of 0.10 was assumed for age-groups 3 and older fish in the model. Instantaneous natural mortality rates of 0.4 and 0.2 were applied to age-groups 1 and 2, respectively. Based on a generalized simulation model, Walters (1969) concluded that natural mortality rates, especially in older fish, could vary widely without affecting harvesting strategies.

Brown and Hennemuth (see footnote 2) reported the size-group structure of fish captured and landed by yellowtail flounder fishermen during 1963. According to these data, few fish less than 250 mm long were captured ($L_{g\min}$ = 250 mm). The modal value of Brown and Hennemuth's capture curve is about 330 mm. The modal value usually coincides closely with the length of complete functional recruitment. Therefore, gear efficiency was assumed to reach its maximum at this length ($L_{g\max}$ = 330 mm). All yellowtail flounder less than 300 mm long were discarded at sea ($L_{m\min}$ = 300 mm) and almost all fish captured of greater than 350 mm were landed ($L_{m\max}$ = 350 mm). Of course, market conditions will change with time and there are now reports of some fish less than 300 mm being landed.

TABLE 2.—Value of each parameter used to yield best results with yellowtail flounder model. The parentheses indicate values used for the model in which recruitment is independent of spawning stock. L_{mi} for $i = 1, 2, \ldots, 7$ are given in Table 3.

Parameter	Value	Description	Source
c_1	0.233×10^{-5}	From weight–length function (Equation (4))	Lux (1969b)
c_2	3.233	From weight–length function (Equation (4))	
c_3	1.26	First quarter seasonal effort factor	Based on quarterly average effort data for 26 to 50 gross ton vessel reported by Lux (1964)
c_4	0.37	Second quarter seasonal effort factor	
c_5	0.87	Third quarter seasonal effort factor	
c_6	1.49	Fourth quarter seasonal effort factor	
c_7	0.725×10^{-6}	From fecundity–length function (Equation (14))	Pitt (1971) for fish from Grand Bank
c_8	4.69	From fecundity–length function (Equation (14))	
c_9	−1.821	From proportion mature–length function (Equation (15))	Based on percent mature data from Royce et al. (1959)
c_{10}	0.00707	From proportion mature–length function (Equation (15))	
c_{11}	0.50	Proportion of females	Data on 9,268 fish provided by Northeast Fisheries Center
c_{12}	−0.68 (−0.89)	Slope of recruitment–temperature factor	From recruitment estimates (Sissenwine 1974), see text
c_{13}	5.8×10^{-6} (60.0×10^{6})	Slope of stock–recruitment function	Fitted to catch data with the model, see text
c_{14}	−0.466	Slope of growth–temperature factor	From annual growth estimates (Sissenwine 1975), see text
q	1.68×10^{-4}	Catchability coefficient	Sissenwine (1974)
L_{g}min	250.0 mm	Minimum size retained by net	From length composition of catch for 1963, see text
L_{g}max	330.0 mm	Size of maximum net retention	
L_{m}min	300.0 mm	Minimum size at which fish are marketed	
L_{m}max	350.0 mm	Size at which all fish are marketed	
T	10.175°C	Mean temperature	National Weather Service data, Block Island
G_1	0.05	Proportion entering size-class 1	Arbitrary
G_2	0.10	Proportion entering size-class 2	
G_3	0.20	Proportion entering size-class 3	
G_4	0.30	Proportion entering size-class 4	
G_5	0.20	Proportion entering size-class 5	
G_6	0.10	Proportion entering size-class 6	
G_7	0.05	Proportion entering size-class 7	
s_m	33.9 mm	Standard deviation of L_m	Data on 9,268 fish provided by Northeast Fisheries Center
k_1	0.56	Growth rate for fish less than 2 yr	See text
k_2	0.285	Growth rate for fish greater than 2 yr	
K_1	0.0	First quarter seasonal growth factor	Based on length by quarter estimates (Lux and Nichy 1969), see text
K_2	0.0	Second quarter seasonal growth factor	
K_3	2.0	Third quarter seasonal growth factor	
K_4	2.0	Fourth quarter seasonal growth factor	
M_1	0.40	Natural mortality of age-group 1	See text
M_2	0.20	Natural mortality of age-group 2	
M_i, $i = 3, 10$	0.10	Natural mortality of age-group 3	

The annual average air temperature at Block Island was used as an index of temperature on the Southern New England ground because there are no water temperature records of adequate length (1944 to present). Block Island is located on the southwest edge of the Southern New England ground.

Taylor et al. (1957) concluded that air temperature data are a rough index of the general level of surface water temperature. Colton (1968) reported that trends in offshore water masses paralleled trends in surface water temperature at Boothbay Harbor, Maine. Lauzier (1965) used trends in air temperature from 1875 to 1905 as an index of the water temperature of the Gulf of Maine. Templeman (1965) concluded that air temperature at St. John's, Newfoundland, and water temperature at Cape Spear for 1952–62 agreed extremely well.

A record of the bottom water temperature at Lurcher Lightship off Nova Scotia (Lauzier and Hull[6]) was collected from 1951 to 1969. The water depth was about 100 m. The correlation between the average annual bottom water temperature at Lurcher Lightship and the average annual air temperature at Block Island is 0.78. The correlation between the annual average air temperature at Block Island and the annual average surface water temperature at Woods Hole, Mass., for data reported by Chase (1967) is 0.87 during the period 1956–66. The correlation between monthly averages of water temperature at Woods Hole and air temperature at Block Island for this 132-mo time series is 0.98. Therefore, Block Island air temperature record was used as an index of water temperature on the Southern New England ground.

The annual equilibrium catch of a fishery is the level of catch that results in no change in the biomass of the nominal stock (stock suitable for

[6]Lauzier, L. M., and J. H. Hull. 1969. Coastal station data temperature along the Canadian Atlantic coast 1921–1969. Fish. Res. Board Can., Tech. Rep. No. 150, 5 p.

landing). The equilibrium catch is the sum of recruitment and growth (of the individual fish of the nominal stock) minus loss due to natural mortality. Based on this relationship using earlier estimates of equilibrium catch and recruitment (Sissenwine 1974) and assuming annual natural mortality of 0.1, Sissenwine (1975) estimated the average annual weight gain per fish of the Southern New England yellowtail flounder fishery for 1944–65. These estimates ranged from 72 to 331 g/fish per year and are significantly correlated (Kendall rank correlation coefficient (τ) of −0.60) with annual average air temperature at Block Island. Estimates of k of the von Bertalanffy function derived from growth increments of age-classes for 1962–71 were also significantly correlated ($\tau = -0.42$) with temperature at Block Island. Thus, the model was designed to simulate the effect of temperature on growth.

The instantaneous growth rate of a fish is related to k by the following equation:

$$\frac{dw}{dt} = kc_1c_2\,(L_m - L)\,L^{c_2-1}. \qquad (19)$$

Equation (19) was derived by substituting Equation (11) into Equation (4) and differentiating with respect to t. For the values of k, c_1, c_2, and L_m reported by Lux (1969b) and Lux and Nichy (1969), dw/dt is 143, 172, 182, and 163 g/yr for a length of 250, 300, 350, and 400 mm, respectively. Most of the fish in the catch are within this range of length. Therefore, only a minor proportion of the estimated range in annual growth per fish can be accounted for by changes in size composition of the stock. Thus, within the constraints of the model described here (c_1, c_2, L_m do not vary with time), k must be nearly proportional to the rate of weight gain.

During the period 1944–65 there were 4 yr in which the estimated average annual air temperature was greater than 11°C and 7 yr in which it was less than 10°C. For the four warmer years, temperature averaged 11.2°C and growth per fish averaged 88 g. For the seven colder years, temperature averaged 9.5°C and growth 222 g. Assuming k proportional to annual average weight gain per year, c_{14} was estimated as −0.466 by solving:

$$\{1 + c_{14}(11.2 - \bar{T})\}/\{1 + c_{14}(9.5 - \bar{T})\} = 88/222.$$

The proportion of yellowtail flounder recruits entering each size category of age-group 1 was assumed as follows: $G_1 = G_7 = 0.05$, $G_2 = G_6 = 0.10$, $G_3 = G_5 = 0.20$, and $G_4 = 0.30$.

Lux and Nichy (1969) reported a value of 500 mm for parameter L_m of the von Bertalanffy growth function for the yellowtail flounder. They selected this value since it was the maximum length observed. The model described in this paper requires values of L_m for each of the seven size categories. Considering the magnitude of s_m (33.9 mm, see Table 2) a value of 500 mm for L_{m4} may yield fish far in excess of the maximum length observed. Therefore, a more conservative value was used: $L_{m4} = 480$ mm.

The probability density function of L_m was used to calculate values of L_{mi} for $i = 1, 2, 3, 5, 6, 7$. The range of values of L_m represented by each size category (Z_{1i} to Z_{2i}) was calculated based on G_i and the normal density table and found to be as in Table 3. The mean value of L_m for each size category equals the integral of L_m times its density function divided by the integral of the density function (results also shown in Table 3).

TABLE 3.—Range and mean for L_m, the maximum length parameter of the von Bertalanffy growth function, representing each of the size categories of the yellowtail flounder model.

Size category	Range of L_m (mm)	Mean of L_m (mm)	Size category	Range of L_m (mm)	Mean of L_m (mm)
1	0.0–425.1	410.9	5	492.8–514.6	503.0
2	425.1–445.4	436.3	6	514.6–534.9	523.6
3	445.4–467.2	457.0	7	534.9–∞	549.1
4	467.2–492.8	480.0			

Lux and Nichy (1969) estimated the growth rate coefficient (k of the von Bertalanffy growth function) for yellowtail flounder older than 2 yr of age as 0.335. For the period during which Lux and Nichy collected their data, the average annual temperature at Block Island was about 9.8°C. This temperature results in a growth-temperature factor (T_g) of 1.175. Lux and Nichy's estimate was divided by T_g resulting in an estimate of $k_2 = 0.285$. An estimate of k_1 (=0.56) was determined using the model so that fish would grow to a realistic length by age 2.

The seasonal nature of yellowtail flounder growth was exhibited when the average lengths of age-groups were determined quarterly (Lux and Nichy 1969). In general, the mean size of an age-group changes little from the first to the second quarter. Thus, most growth apparently occurs during the second half of the year. In order

to simulate this phenomenon, the following quarterly growth adjustment factors were used: $K_1 = K_2 = 0.0$ and $K_3 = K_4 = 2.0$.

Estimation of c_{12} of the recruitment–temperature factor (T_r, Equation (16)) depends on the form of the recruitment relationship that is assumed. The parameter c_{12} was estimated for both the linear and density independent recruitment functions (Equations (17) and (18)) using estimates of annual recruitment reported by Sissenwine (1974). During 1949–53, recruitment averaged 6.82 million fish (recruits to the stock of marketable fish, about 3 yr and older) with a spawning stock size proportioned to an average relative abundance of 1.4 tons/day and an average annual temperature of 11.08°C. On the other hand, for 1960–63, recruitment averaged 49.7 million fish with a relative abundance and annual average temperature of 2.9 tons/day and 9.65°C, respectively.

For the density independent recruitment function, fluctuations in recruitment result directly from fluctuations in T_g. An increase in recruitment and in T_g by a factor of 7.3 while the temperature anomaly changes from 0.905 to −0.525 provides an estimate of $c_{12} = -0.89$ by solving the following expression:

$$7.3\{1 + c_{12}(0.905)\} = 1 + c_{12}(-0.525).$$

If egg production is assumed proportional to stock size or relative abundance, then for the linear recruitment function, the increase in recruitment by a factor of 7.3 would reflect an increase in spawning stock size by a factor of 2.05 (≈2.9/1.4) and an increase of T_g by a factor of 3.56 (≈7.3/2.05). Therefore, solving the following expression:

$$3.56\{1 + c_{12}(0.905)\} = 1 + c_{12}(-0.525)$$

$c_{12} = -0.68$ for the linear recruitment function.

Since little is known about the survival of yellowtail flounder eggs and their eventual recruitment to age-group 1, c_{13} of the recruitment function was estimated by fitting the model to data (see Verification). The parameter c_{13} was estimated as 5.8×10^{-6} (fish per egg) for the linear recruitment model and as 60.0×10^6 (fish) for the density independent recruitment model.

Both estimates appear realistic as indicated by the following discussion. The average recruitment to the stock of marketable fish reported by Sissenwine (1974) was 22.8×10^6 fish. Assuming an instantaneous natural mortality of 0.4 for age-group 1 and a natural mortality of 0.2 with a total gear mortality of 0.5 ($F + D$) for age-group 2, recruitment to age-group 1 may be crudely estimated by multiplying recruitment to the marketable stock by 3.0. Thus, average annual recruitment to age-group 1 could be estimated as 68.4×10^6 fish which is similar to the estimate of c_{13} for the density independent model. For the linear recruitment model, c_{13} is the proportion of eggs that survive to be recruited to age-group 1 under average temperature conditions. Using the average catch per effort for 1943–66 ($U = 2.5 \times 10^6$ g/day), the sex ratio ($c_{11} = 0.5$), the catchability coefficient ($q = 1.68 \times 10^{-4}$), and an estimate of average weight and fecundity (of females) of the nominal stock ($W = 451$ g, $Fe = 700{,}000$ eggs), c_{13} could be crudely estimated as 5.9×10^{-6} using $c_{13} = (R \cdot W \cdot q)/(Uc_{11} \cdot Fe)$. For the winter flounder, *Pseudopleuronectes americanus*, Saila's (1961) work indicated about 18 recruits to age-group 1 per million eggs (actually reported 18 recruits/100,000 hatched eggs assuming 10% hatching success). The value used here is somewhat lower, but the fecundity of the yellowtail flounder is higher than for the winter flounder.

In order to avoid the possibility of recruitment becoming negative for extremely high temperatures, the additional constraint that recruitment never falls below 5 million fish was incorporated into the model.

The initial length and number of individuals of each age–size compartment had to be specified prior to simulating the fishery. Royce et al. (1959) reported the mean length of age-groups 2–6 for the first quarter of 1943. These values were assumed as the initial length of size category 4 of the appropriate age-groups. For the initial lengths of the other age-groups, reasonable but arbitrary values were selected. The average initial size of each age-group is listed in Table 4. The lengths of size categories 1, 2, 3, 5, 6, and 7 were determined by multiplying the length of size category 4 by 0.856, 0.908, 0.950, 1.050, 1.092, and 1.144, respectively. These factors correspond to the ratio of the maximum length of each size category to the maximum length of size category 4.

The onset of the collection of fishing effort data was 1943; therefore, the model was used to simulate the fishery from that date. The relative abundance of the yellowtail flounder during the first quarter of 1943 was 5,742 fish/day (Royce et al.

TABLE 4.—Initial (1 January 1943) mean total length in millimeters of each age-group for yellowtail flounder model. The lengths of age-groups 2–6 were reported by Royce et al. (1959).

Age-group	Mean length (mm)	Age-group	Mean length (mm)
1	160	6	401
2	271	7	425
3	324	8	440
4	353	9	450
5	372	10	460

1959). Dividing this by q, the mean population size during this quarter was estimated as 34.2×10^6 fish. Because there is little growth and, therefore, little recruitment during the first quarter (since fish are recruited as they grow to the size vulnerable to fishing gear), the population was assumed to undergo exponential decay during this time interval. The effort expended during the first quarter of 1943 was 2,038 days (Royce et al. 1959), resulting in a total maturity $Z = 1.47$ ($Z = M + qf$ where f is the rate of fishery in days per year). Accordingly, the size of the landable stock at the beginning of 1943 was estimated as about 41.1×10^6 fish (using Equation 1.38 of Ricker (1975) modified for an interval of one-quarter of a year).

Royce et al. (1959) also reported the age composition for the first quarter of 1943. The catch primarily comprised fish greater than 3 yr of age. The number of fish captured per day for age-group 3 and older is shown in Table 5. Based on the

TABLE 5.—Catch per day and relative abundance adjusted for fishing vulnerability of age-group 3 and older yellowtail flounder for the first quarter of 1943. These age-groups represented 95% of the catch.

Age-group	Catch/day	Adjusted relative abundance
3	1,793	3,984
4	1,596	1,995
5	1,008	1,061
6	504	504
7+	476	476

length composition assumed for each age-group and Equation (9), the relative level of fishing mortality suffered by fish of age 3, 4, 5, and older was calculated as 0.45, 0.80, 0.95, and 1.00, respectively. By dividing the catch per day of each age-group by the appropriate factor, the relative abundance adjusted for fishing vulnerability was obtained (also Table 5). These values represent the relative abundance of each age-group in the population. Using Table 5,

$$N_{4.} = 0.50\ N_{3.}$$

$$N_{5.} = 0.55\ N_{4.} = 0.280\ N_{3.}$$
$$N_{6.} = 0.48\ N_{5.} = 0.130\ N_{3.}$$
$$N_{7.} = 0.50\ N_{6.} = 0.065\ N_{3.}$$
$$N_{8.} = 0.50\ N_{7.} = 0.033\ N_{3.}$$
$$N_{9.} = 0.50\ N_{8.} = 0.016\ N_{3.}$$
$$N_{10.} = 0.50\ N_{9.} = 0.008\ N_{3.}$$

where the subscript . indicates the summation over all size categories, and the survival of fish older than 7 yr was assumed to be 0.50. The size of the marketable population was estimated by summing N_i times the relative fishing vulnerability of age-group i. This expression was set equal to 41.1×10^6 fish and solved for $N_{3.}$ ($\approx 32.0 \times 10^6$ fish). Estimates of initial conditions for other age-groups were obtained using the equations in this paragraph. Age-group 2 was assumed to be twice age-group 3 as indicated by a natural mortality of 0.2 and a discard mortality of about 0.5. Based on a natural mortality of 0.40 age-group 1 was assumed to be 1.5 times age-group 2. The initial conditions of each age-group for the beginning of 1943 based on the above discussion are shown in Table 6. The population was distributed among the size categories according to the appropriate values of G_i.

TABLE 6.—Initial size of each age-group of yellowtail flounder population assumed at the beginning of 1943.

Age-group	Number in thousands	Age-group	Number in thousands
1	95,000	6	4,200
2	64,000	7	2,100
3	32,000	8	1,100
4	16,000	9	530
5	8,800	10	260

VERIFICATION

The primary mode of verification of the model was to compare predicted annual levels of catch with published values. Lux's (1969a) record of catch and fishing effort for 1943–66 is in conflict for several years with data reported by Brown and Hennemuth (see footnote 2) in an unpublished form. These conflicts are minor, except for the 1966 catch where the difference is about 40%. Since this year is at the end of the published record and could easily be ignored, 1943–65 were initially used for verification. After c_{13} was fit to the data, the model was then compared with data through 1972.

Before comparing the model with the published data, it was necessary to select a time step or

integration interval that would not result in unreasonable numerical errors being propagated through many years of simulated time. This was done by increasing the time step until the simulation results converged. With an integration interval of 0.005 yr, the results converged sufficiently so that a numerical error of less than 5% is expected after 23 yr of simulation (the length of the data record used for verification). This level of error was considered acceptable in light of the precision of all the data upon which this work was based. It was noted that each decrease in the time step was accompanied by an increase in the simulated catch; therefore, the predictions yielded by the computer simulations are probably slightly lower than would have resulted from an exact solution of the model.

The average length of age-groups 2–5 according to the model for 1943–66, 1957–62, and 1962–71, and the average length of these age-groups as reported by Lux and Nichy (1969), and of the catch for 1962–71 are compared in Table 7. Age-groups 2–5 were considered because they were most abundant in available samples; and, therefore, their means have smaller standard errors than less abundant age-groups.

Most of the fish measured by Lux and Nichy were collected during 1957–62. Model results for this period compare favorably as expected since the model was designed to simulate the situation reported by Lux and Nichy. The average simulated lengths for 1943–66 are generally lower than for the 1957–62 design period since the design period had a lower temperature (favorable to growth) than the longer time interval.

The model tends to overestimate growth for 1962–71. The mean length of fish of a particular age-group collected from the catch for 1962–71 is lower than is predicted by Lux and Nichy's growth function. This situation cannot be explained as an effect of temperature. As has been the practice throughout this work, the model was designed in accordance with the published literature; therefore, some apparent overestimation of growth in later years of the simulations is inevitable. This situation makes application of the model less satisfactory for recent years, but part of the effect of overestimating growth would be compensated for by a shift in age-group structure of the catch. If the model slightly overestimates growth, there is a tendency to catch younger fish; and, therefore, the effect of overestimating growth is partially offset.

The simulated size-category structure of captured (landed and discarded) fish for 1943–65 is compared with unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2) in Figures 2 and 3. Clearly, it would have been

TABLE 7.—Average length (millimeters) of yellowtail flounder age-groups 2–5 according to the model for 1943–66, 1957–62, and 1962–71 according to Lux and Nichy (1969), and for samples from the commercial catch collected January–March 1962–71 (data provided by Northeast Fisheries Center).

Age-group	Model 1943–66	Model 1957–62	Model 1962–71	Catch samples 1962–71	Lux and Nichy
2	275	290	323	306	266
3	303	338	365	342	338
4	351	367	397	365	378
5	378	385	416	387	404

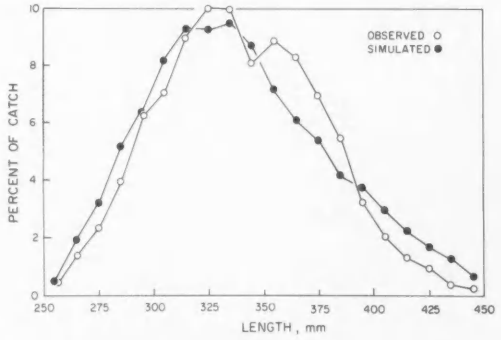

FIGURE 2.—Simulated (1943–65) and observed (unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2)) size-category structure of catch (including discards) of yellowtail flounder.

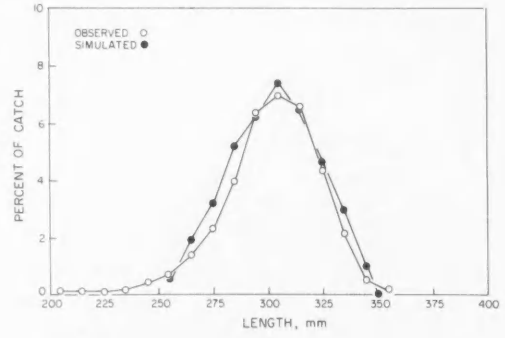

FIGURE 3.—Simulated (1943–65) and observed (unpublished data for 1963 as reported by Brown and Hennemuth (see footnote 2)) size-category structure of discards as percentage of catch (including discards) for yellowtail flounder.

better to compare the 1963 simulated size-category structure with these data, but, because of a programming oversight, this information was not available. The comparisons in Figures 2 and 3 are generally favorable and indicate that the assumed linear relationships (Equations (6) and (7)) describing the relative effectiveness of the fishing gear and the marketability of fish as a function of length were adequate. The model indicates that 39.5% of the fish captured by fishermen for 1943–65 were discarded. The average weights of landed and discarded fish based on Figures 2 and 3 are 455 and 249 g, respectively.

The parameter c_{13} of the recruitment function (Equations (17) and (18)) was estimated by running the model for several values of this parameter and selecting the value that explained the greatest proportion of variation in observed yield. Of the values considered, c_{13} equal to 60.0×10^6 and 5.8×10^{-6} for the density independent and linear recruitment models were most successful in explaining variation in yield. Since only a finite number of values of c_{13} were considered, the values selected are probably not the "best least squares" estimates, but the results (Table 8) indicate that the model is not very sensitive to 5–10% fluctuations in this parameter. As noted earlier, these values appear realistic.

TABLE 8.—Percent of variation in yield explained by the yellowtail flounder model with various values of c_{13} for 1943–65.

c_{13}	Linear stock-recruitment (%)	c_{13}	Density independent stock-recruitment (%)
5.4×10^{-6}	73.6	55.0×10^6	81.3
5.6×10^{-6}	82.0	57.5×10^6	82.6
5.7×10^{-6}	84.5	60.0×10^6	83.2
5.8×10^{-6}	85.5	62.5×10^6	83.0
6.0×10^{-6}	82.3	65.0×10^6	82.1
		70.0×10^6	78.1

The model using linear or density independent recruitment explained 85.5 and 83.2% of the variation in yield from 1943–65, respectively. In addition to catch and effort data reported by Lux (1969a), catch data through 1972 and effort data through 1971 were available (at the time when this research was in progress) for the Southern New England ground (Brown and Hennemuth see footnote 2; Brown see footnote 3; and Parrack see footnote 4). Both the linear and density independent stock-recruitment models were run for 1943–72 (assuming that the level of effort was unchanged from 1971 to 1972), and the results were compared with the available data in Figures 4 and 5. Both models seem to simulate catch as well since 1965 (although yield is substantially underestimated for 1969 and 1970) in spite of the fact that they were developed independently of the later data and that growth is apparently somewhat overestimated toward the end of the simulation. Since errors for any particular

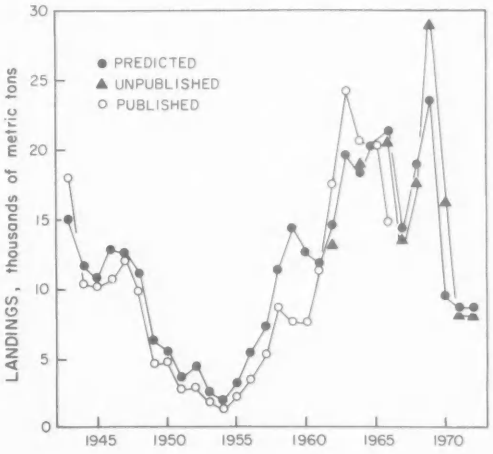

FIGURE 4.—Landings of Southern New England yellowtail flounder as reported in published and unpublished reports and predicted by the model with linear recruitment function (Equation (17)).

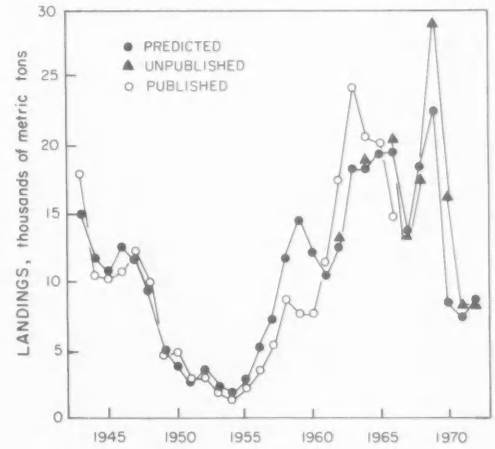

FIGURE 5.—Landings of Southern New England yellowtail flounder as reported in published and unpublished reports and predicted by the model with a density independent recruitment function (Equation (18)).

year are propagated through the simulation, it is surprising that the model seems to recover after occasional substantial deviations from the observed yield.

Sissenwine (1974) explained most of the variability in recruitment of the Southern New England ground even though the size of the spawning stock was ignored. This earlier work noted that spawning stock size may have an important effect on recruitment, but the effect might be obscured by environmental noise. The work reported here demonstrates that models incorporating either linear or density independent recruitment explain most past variability in catch of the fishery. Nevertheless, the model incorporating recruitment linearly dependent on spawning stock size is preferable for the following reasons:

1. While the linear model only explained 2.2% more variation than the density independent model, it did explain 13% of the density independent model's residual variation with no increase in number of parameters.
2. While the density independent model is more simplistic mathematically, a direct linear relationship between stock size and recruitment is a more basic biological relationship. Obviously, recruitment cannot be independent of spawning stock size over its entire range. The density independent situation can only exist as a special case of a more complex nonlinear stock-recruitment relationship.
3. It seems unrealistic for recruitment to be unaffected by size of spawning stock when stock size varies by a factor of 3.
4. The linear stock-recruitment model is a more conservative management tool than the density independent model. Management practices designed to prevent a dangerous reduction in stock size of a population regulated by a linear stock-recruitment relationship will also prevent a reduction in stock size of a population regulated by a density dependent stock-recruitment relationship.

No attempt was made to use the Ricker (1954, 1958) stock-recruitment function or other nonlinear functions because the results obtained using the linear and density independent functions (Equations (17) and (18)) indicated that most likely these more complicated functions would not significantly increase the accuracy of the model. When using the linear model where the Ricker function (for example) is more appropriate, the linear model is expected to be accurate at low population levels but overestimates recruitment (and catch) at higher population levels. The reverse situation is expected when the density independent model is used where a Ricker function is more appropriate. In neither case was the more complex Ricker function indicated.

Based on the above discussion, the linear stock-recruitment function (Equation (17)) seemed most appropriate over the observed range of population size. Therefore, only the linear model is used in the remainder of this paper.

The linear stock-recruitment model was run for 1943–65 without temperature dependent growth ($c_{14} = 0.0$), without temperature dependent recruitment ($c_{12} = 0.0$), and without temperature dependent growth or recruitment ($c_{12} = c_{14} = 0.0$). None of these situations explained a significant portion of variation in catch. This fact does not constitute rigorous evidence that incorporation of T_g and T_r into the model is necessary to explain most of the variability in catch because no attempt was made to tune the model for the temperature independent cases. Earlier work by Sissenwine (1974, 1975) demonstrated the influence of temperature on the fishery and supports the incorporation of T_g and T_r into the model.

APPLICATIONS

The effects of several alternative fishing strategies were examined using the model. These examples deal with some aspects of the model which are not common components of other fishery models (such as discard mortality, temperature dependence, and seasonal growth and fishing rate).

The impact of discarding at sea fish shorter than 300 mm was evaluated by running the model with the assumption that the minimum size retained by a net equaled this value. The results for $L_{g\min} = 300$ mm are compared with the model results as described earlier ($L_{g\min} = 250$ mm) in Figure 6. Landings in excess of 30,000 metric tons are not shown because these have not been observed during the history of the fishery; thus simulations indicating these high values are extrapolative in nature. These higher simulated landings result because the model assumes a linear stock-recruitment relationship at all stock sizes, while in reality the relationship probably becomes density dependent as stock size becomes large. By eliminating discard mortality of fish shorter

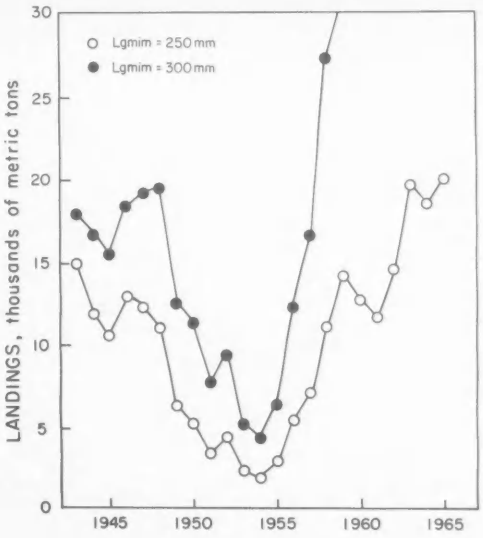

FIGURE 6.—Simulated landings of yellowtail flounder with L_{gmin} = 250 mm and 300 mm. Landings greater than 30,000 metric tons are not shown.

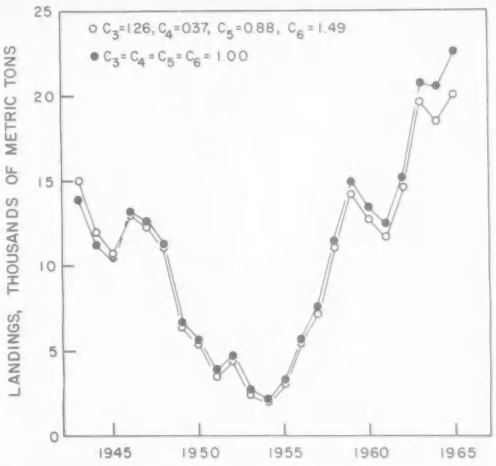

FIGURE 7.—Simulated landings of yellowtail flounder with fishing effort applied uniformly and with c_3–c_6 as assumed for 1943–65.

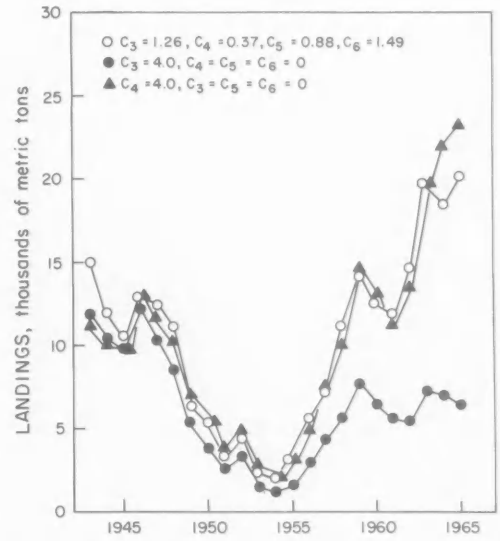

FIGURE 8.—Simulated landings of yellowtail flounder with all fishing effort in the first or second quarter of the year and with c_3–c_6 as assumed to have occurred for 1943–65.

than 300 mm, these fish have a higher probability of surviving until they are recruited and spawn. The result was from a 20% to a severalfold increase in landings.

Using the Beverton and Holt yield per recruit (YPR) function, Brown and Hennemuth (see footnote 2) found less than a 40% increase in yield by delaying the age at first capture from 1.75 yr (or 245 mm) to 2.5 yr (or 302 mm) for F less than 1.1. This was the highest simulated fishing mortality rate during 1943–65. The substantially greater increase in yield from the simulation reported in Figure 6 results from increased recruitment which is not considered in the Beverton and Holt YPR function.

The benefit of increasing mesh size to eliminate discard mortality is clearly demonstrated (for the linear recruitment model), but this analysis ignores financial and technological difficulties which may be involved (Gates and Norton 1974).

The effect of the seasonality of fishing mortality was explored by varying seasonal effort adjustment factors (c_3, c_4, c_5, and c_6). Situations where effort was applied uniformly throughout the year and where all effort was applied during a single quarter were considered. These cases are compared with the results reported earlier (c_3 = 1.26, c_4 = 0.37, c_5 = 0.88, and c_6 = 1.49) in Figures 7–9 and Table 9.

The simulations reported in Figures 7–9 indicated that the seasonal aspect of the expenditure of effort and resulting fishing mortality could

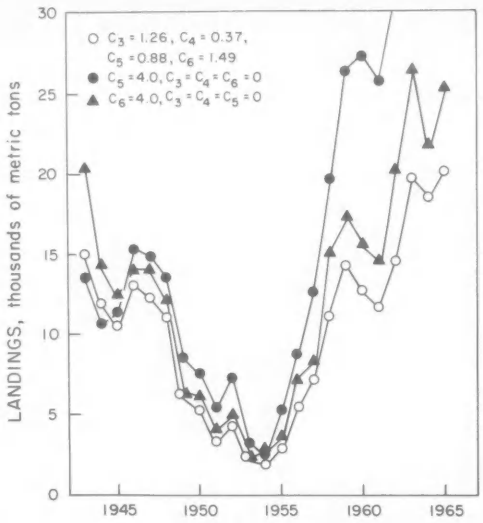

FIGURE 9.—Simulated landings of yellowtail flounder with all fishing effort in the third or fourth quarter of the year and with c_3–c_6 as assumed to have occurred for 1943–65.

TABLE 9.—Comparison of simulated catches of yellowtail flounder with various values of the seasonal effort factors (c_3, c_4, c_5, c_6). Percentage changes in yield are relative to the simulated yield with c_3, c_4, c_5, and c_6 as in the first line of the table.

				Percentage change in yield		
c_3	c_4	c_5	c_6	1943	1944	1943–65
1.26	0.37	0.88	1.49	—	—	—
1.00	1.00	1.00	1.00	−6.7	−4.5	+3.6
4.00	0.0	0.0	0.0	−20.7	−14.3	−40.6
0.0	4.00	0.0	0.0	−24.0	−16.8	−0.6
0.0	0.0	4.0	0.0	−9.4	−9.3	+92.8
0.0	0.0	0.0	4.0	+36.4	+21.0	+22.6

have a very significant impact on the yield of the fishery. There was little change in yield indicated when fishing mortality was assumed uniform throughout the year. The simulations showed that yield of the simulated fishery would have been reduced if all fishing mortality occurred during the first quarter of the year. If all fishing mortality were applied during the second quarter, yield of the fishery would have been lower during the first few years of the simulation, but little difference in total yield is indicated over 23 yr. The expenditure of effort during the third quarter also tended to reduce the early catch, but in the long run appeared to result in the highest yield. By restricting fishing mortality to the fourth quarter of the year, some initial increase in catch was indicated and long-term yield was also increased.

These results reflect the facts that spawning occurs during the second quarter and growth of fish is limited to the third and fourth quarters of the year according to the model. Clearly, to obtain a short-term gain in yield, it is most advantageous to harvest at or near the end of the growing season (Table 9). Long-term gains were obtained when egg production was optimized by harvesting just after spawning (third quarter). By concentrating effort during the fourth quarter, an increase in yield was indicated for all years of the simulation. Fishing during the first quarter appears to be particularly detrimental because it crops fish just prior to spawning.

The seasonal pattern of effort exhibited by the fishery in the past includes intense fishing during the first quarter and the fourth quarter of the year. Apparently these balance, resulting in yields similar to the case where fishing is uniform through the year. In recent years, the annual catch quota for the United States (established by the International Commission for the Northwest Atlantic Fisheries (ICNAF)) was divided equally among the four quarters. The result is that fishing mortality was probably distributed nearly uniformly through the year. There may be some advantage to increasing the portion of the annual quota captured during the second half of the year. It is important to note that the long-term gains obtained by concentrating fishing just after the spawning season will not be realized if recruitment is independent of spawning stock size (Equation (18)).

Several experiments were conducted with the model in order to determine to what degree the yield of the fishery could be stabilized or increased by regulating the annual expenditure of effort and ultimately F. For a fishery in which recruitment is linearly related to stock size, in the long run it is advantageous to reduce fishing effort (and mortality) in order to increase egg production. Therefore, the fishery was simulated with effort at 80% of observed values (Figure 10). The short-term decrease in yield was rather minor. Considerable long-term advantage was predicted; but even with a reduced level of effort, the simulated fishery declined during the late 1940's and early 1950's. However, the recovery when conditions became favorable was more rapid at the lower level of effort for this particular case.

The Beverton and Holt YPR equation (Brown and Hennemuth see footnote 2) indicates less than a 5% increase in catch with a 20% decrease in

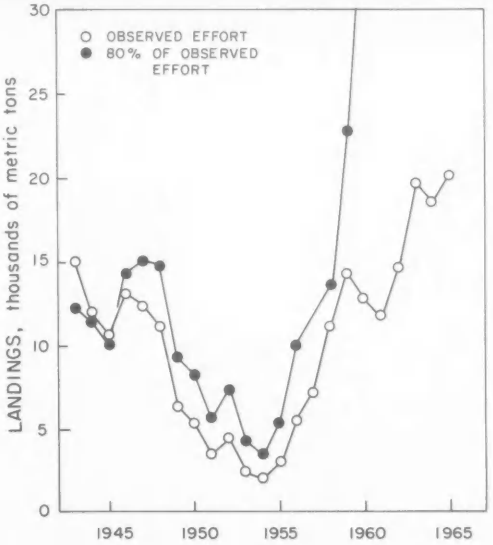

FIGURE 10.—Simulated landings of yellowtail flounder with observed level of fishing effort and with 80% of the observed level.

fishing mortality (for $0.6 \leq F \leq 1.5$ and age at first capture between 1.75 and 3.0). Therefore, most of the increase in yield indicated in Figure 10 must result from improved recruitment at lower levels of F.

Since recruitment and growth appear related to temperature, the possibility of using this environmental variable to predict an appropriate level of effort was considered. The model is such that growth and recruitment are proportional to T_g and T_r, respectively. Therefore, the following relationship between fishing effort and T_g and T_r was utilized:

$$f_i = c_{15} \cdot \{(T_g)_{i-1} + (T_r)_{i-2}\}. \qquad (20)$$

Effort for year i was based on the growth–temperature factor for the year $i - 1$ since Equation (20) is of little value unless effort can be set in advance. The recruitment–temperature factor from 2 yr prior ($i - 2$) was used since recruitment lags spawning by about 2 yr. A 3-yr lag could have been used. T_g and T_r could have been weighted in Equation (20) since the latter is usually more important in determining equilibrium yield, but this would have introduced another parameter.

Initially, c_{15} was estimated as 1,870 days of fishing, which yields about the average level of effort for 1943–65 when T_g and T_r equal 1. A value higher and lower than 1,870 days was also considered. Simulated catches for each value of c_{15} are shown in Figures 11–12, and the simulated catch per unit of effort is shown in Figure 13.

For 1943–65, c_{15} = 2,200 days resulted in a decrease in relative abundance while c_{15} = 1,540 days permitted the relative abundance to increase. The value of c_{15} (1,870 days) corresponding to the average effort during 1943–65 best stabilized the relative abundance of the fishery, but was only slightly more effective than the voluntary actions of the fishermen who probably responded to fluctuations in fishing success (U). It appears that a function even more sensitive to temperature than Equation (20) is required to better stabilize the population. Since T_r is more sensitive to temperature than T_g, weighting of these factors (in favor of the former) might result in a function more effective in maintaining the population size during the early 1950's. Nevertheless, the yield of the simulated fishery (with the linear recruitment function) could have been substantially increased if fishing effort were regulated by a simple function such as Equation (20) with c_{15} considerably less than 1,870 days.

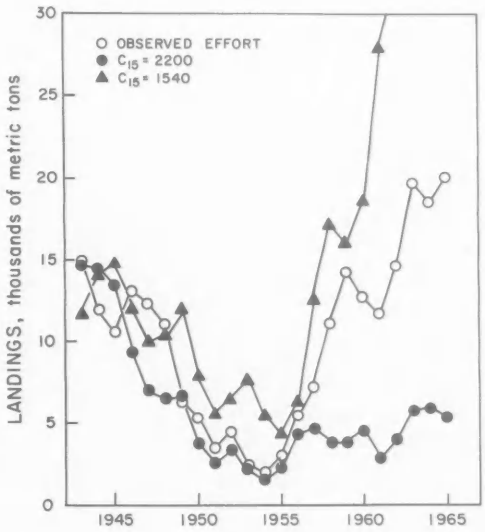

FIGURE 11.—Simulated landings of yellowtail flounder with observed effort and with effort set by Equation (20) using c_{15} = 2,200 or 1,540.

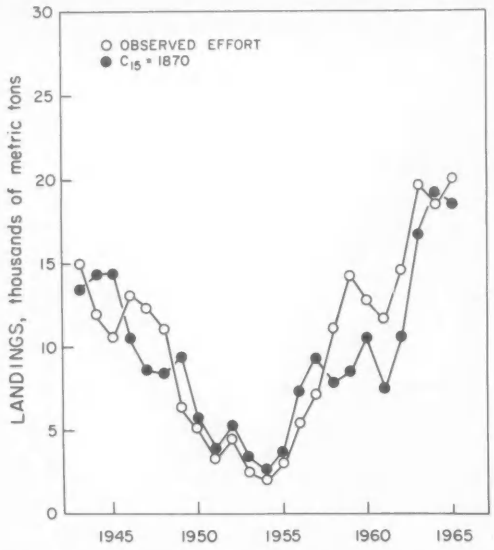

FIGURE 12.—Simulated landings of yellowtail flounder with observed effort and with effort by Equation (20) using c_{15} = 1,870.

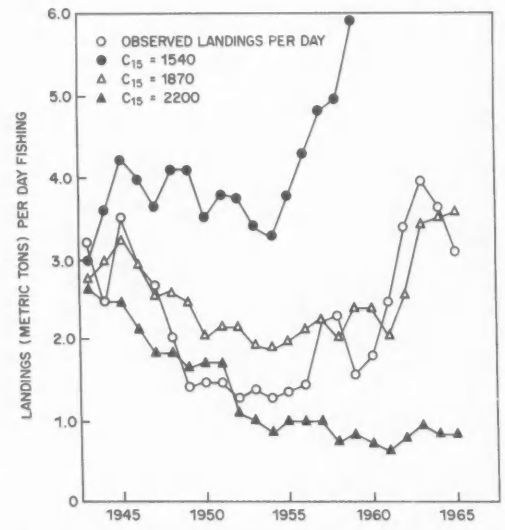

FIGURE 13.—Observed catch of yellowtail flounder per day of fishing and simulated catch per day with effort set by Equation (20) using c_{15} = 1,540, 1,870, or 2,200.

At present, annual catch quotas for the Southern New England yellowtail flounder stock are based on a prerecruit index (Brown and Hennemuth 1971). The index is calculated from the catch of 1-yr-old fish in an autumn bottom trawl survey (Grosslein 1969). Thus the major source of variability in production resulting from the influence of temperature on recruitment is accounted for in current stock assessments. This model should not be considered as an alternate method of management of the fishery on a year to year basis without further verification and refinement.

Walters (1969) developed a yield optimization procedure for his generalized fish simulator using the steepest ascent method. The development of an optimization procedure for the model reported in this paper would be more difficult because this model is driven by two exogenous factors, temperature and the rate of fishing, while Walters's model is only driven by fishing mortality. This model is generally more complex than Walters's model and much more expensive to run. Therefore, the development of an optimization procedure is beyond the scope of the present work.

DISCUSSION

A complex compartmentalized simulation model of the Southern New England yellowtail flounder fishery has been described, verified against catch statistics, and used to examine methods of increasing yield. The relationships and parameters upon which the model was based do not appear to be unreasonable since most variability was explained. Nevertheless, in retrospect, some consideration of alternate approaches to estimating parameters and of modifications of the model is appropriate. It is important to remember that there may be numerous other models or parameter values equally as successful at explaining variation in catch as the one proposed here.

An average maximum length (L_{m4}) for the simulated population of 480 mm was assumed. This value was used in order to assure that few fish would exceed 500 mm in length. When fishing pressure was applied to the simulated population, its average maximum length was suppressed. For some years, the average length of the older age-groups converged to about 460 mm. Since the growth rate coefficients (k_i) of adult fish were based on Lux and Nichy's (1969) work where a maximum length of 500 mm was assumed, the model tends to underestimate the length of older fish. In order to compensate for this effect, the growth rate coefficient of fish younger than 2 yr of age was overestimated. The result was that

the mean size of younger fish was higher than observed while the converse applied to older fish. The differences were generally small. The sizes of the most abundant fish in the catch (age-groups 3 and 4) were well simulated. While the model adequately simulates growth, more precise results might have been obtained by assuming an average maximum size in excess of 500 mm. The result, with fishing, would be an average maximum size near the value assumed by Lux and Nichy (1969). Thus the assumed value of k_2 would have been more appropriate.

The parameters of c_{12} and c_{14} specify the temperature dependence of the model. Estimates of these parameters were based on Sissenwine's (1974, 1975) calculations of recruitment and average growth per fish for 1944–65. No attempt was made to improve these estimates by tuning them to the model. While Figures 4 and 5 indicate the adequacy of the model and its parameters, these figures also reveal that catch was generally overestimated during warm years and underestimated during cold years. This implies that the fishery was probably more sensitive to temperature than indicated by estimates of c_{12} and c_{14}. Rather minor adjustment of these parameters would probably account for much of the remaining unexplained variation in catch. On the other hand, since tuning in effect reduces the residual degree of freedom and, more subjectively, reduces confidence in the model, no attempt was made to improve the initial estimates of c_{12} and c_{14}.

Adult female yellowtail flounder are generally longer than males of the same age. The model does not distinguish between sexes. To do so would require doubling the central processing time required to run the model. Fishing pressure would tend to shift the sex ratio in favor of males because of this size difference. Since the sex ratio ($c_{11} = 0.5$) was estimated for the exploited population, the influence of fishing was incorporated into the model through the estimation of this parameter. Variations in c_{11} resulting from changes in level of fishing were not simulated.

Since females are larger than males, the total fecundity of the population is underestimated when based on the mean size of the age–size compartments. This bias is probably compensated for by overestimating mean recruitment per egg (c_{13}). Thus, expansion of the model to segregate fish according to sex should not affect the results reported here, although some revision of c_{13} would be required.

In recent years, several changes have occurred in the Southern New England yellowtail flounder fishery that were not reflected in the model. During the late 1960's, more active industrial and distant water fisheries (using small mesh nets) for the yellowtail flounder developed. The fisheries statistics used in this report do not include the catch of the industrial fishery which in a few years equaled 20% of the total yield. Estimates of the catch of the distant water fishery are included and the fishing effort of the distant water fleet is estimated by assuming that the catch per unit effort was the same as for the domestic fishery. Since 1971, the fishery has been regulated by quotas set by ICNAF. During the 1970's, landings of yellowtail flounder within ICNAF Subarea 6 (south of the Southern New England ground which is within ICNAF Subarea 5) have increased. The relationship between the fisheries in these two areas is unknown (Brown see footnote 3; Parrack see footnote 4). These recent changes necessitate several modifications of the model before it can be used to simulate the present fishery.

The work reported here indicates the potential for predicting future trends of certain well-studied fisheries in which the role of a specific environmental variation can be described. Two important limitations of this approach are demonstrated. Firstly, model parameters may change with time; thus it is important to keep the model up-to-date. This does not imply that the model should be regularly tuned to assure that it successfully predicts each additional year of data but rather that parameters be updated as evidence of change in the fishery becomes available. Secondly, numerous fundamentally different models may be nearly as successful in simulating a specific system. Therefore, it is dangerous to limit consideration to a single model or regulatory mechanism.

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INCOME ESTIMATES AND REASONABLE RETURNS IN ALASKA'S SALMON FISHERIES[1]

JAMES E. OWERS[2]

ABSTRACT

Earnings in some fisheries may fall to a level that is unacceptable from the viewpoint of public policy. Using the Alaska salmon fisheries as an example, this paper examines a method for establishing the number of operating units that will provide a reasonable economic return in a fishery. Estimates are provided of the rates of return that can be expected with various numbers of operating units. Three criteria are then developed to determine a reasonable rate of return. These criteria include: 1) a comparison with wages in a similar industry in an equal time period, 2) a comparison with total annual incomes from all sources with total incomes of workers in other occupations, and 3) an estimate provided by fishermen themselves. These three different measures indicate an optimum number of operating units within a fairly narrow range. In some fisheries it appears that substantial reductions in the number of fishing units will not be sufficient to raise incomes to an "acceptable" level. This raises questions about the allocation of valuable fishery resources among various user groups.

During the last two decades economists have developed a general theory of a common property fishery under conditions of open access. The salient implications of that theory are that: 1) there is a danger that the resource will be fished beyond maximum sustained yield, 2) the resource will not be harvested with maximum economic efficiency, and 3) there will be a misallocation of productive factors between the fishing sector and other sectors of the economy (Crutchfield and Pontecorvo 1969). Empirical research has shown that there may be a fourth consequence of open access that is not adequately dealt with in the theoretical literature. This is the fact that earnings of fishermen under conditions of open access may fall below a level that is acceptable from the viewpoint of public policy (Sinclair 1960; Owers 1974; Huq[3]; Smith[4]). The public interest arises from the fact that poor earnings have been responsible for creating sanitation, health, safety, and other hazards; that programs providing government assistance for fishermen are becoming increasingly expensive; and that in many cases commercial users can no longer afford to pay their share of management costs. The cause of the problem appears to be the very low opportunity costs of fishermen who have only an avocational interest in fishing or else have little mobility and limited access to alternative employment.

Data collected by interview and from landing records indicate that 44% of the purse seiners, 15% of the drift gill netters, and 60% of the set gill netters in Alaska showed a net loss in 1973 (Smith et al.[5]). In the same year, the average net return to the more than 6,400 gear operators who participated in those salmon fisheries which now have limited entry was about $1,600 per gear operator.

Recognition of the recurring problems created by low earnings in many of the state's fisheries led Alaska to pass the first comprehensive limited entry law in the United States in 1973. The law directs an independent commission to stabilize or reduce the number of legal units of gear that can be fished in those fisheries where economic or biological conditions require it. Specifically the law states the following must be considered in establishing an economically sound number of entry permits: "The number of entry permits sufficient to maintain an economically healthy fishery that will result in a reasonable average

[1]The opinions and conclusions set forth in this paper are not those of the Commercial Fisheries Entry Commission nor the State of Alaska.

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[3]Huq, A. M. 1971. A study of the economic impact of changes in the harvesting labor force in the Maine lobster fishery. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., contract 14-17-007-1121, Wash., D.C., 34 p.

[4]Smith, F. S. 1974. 1972 commercial fishermen survey. Dep. Agric. Econ., Oreg. State Univ., Corvallis, 7 p.

[5]Smith, F. S., D. Liao, J. Martin, and P. Adelman. 1975. Profitability analysis for Alaska fishing businesses. Dep. Agric. Econ. Oreg. State Univ., Corvallis, 13 p.

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rate of economic return to the fisherman participating in that fishery considering time fished and necessary investments in vessels and gear . . . (Anonymous 1973a)." As used in the law and this discussion, a "fishery" refers to a specific combination of species, gear type, and management district. Figure 1 shows the salmon management districts in the state. An entry permit entitles the holder to operate a legal unit of gear in a fishery.

In 1974 entry was limited in the power troll fishery and all salmon net fisheries, with the exception of those in the Arctic, Yukon, and Kuskokwim management districts. This paper examines a procedure that can be used to evaluate the gear cutbacks that may be required to achieve "reasonable" earnings in these fisheries. Because the limited entry law seeks to achieve a balance among social objectives, biological management, and economics, the reductions suggested here, which consider only possible economic objectives, are not necessarily those which the law would require.

A detailed discussion of sample size, methodology, and other factors affecting the validity of data used can be obtained from several of the references cited at the end of the article. Further elaboration is not provided in the text, other than to briefly describe the data used and its source. It should be further recognized that it is not the purpose of this paper to present a rigorous mathematical definition of a problem, but rather to point out its general magnitude and direction.

ESTIMATING EXPECTED RETURNS IN THE SALMON FISHERIES

Several equations were used to estimate returns salmon fishermen might receive with various numbers of operating units in the fisheries. All the equations are presented below, followed by a more detailed description of the variables. Table 1 summarizes the input data used in the equations. To estimate gross returns per operating unit in each fishery, the following equation was used:

$$G = \frac{T \cdot (1 + S)}{P \cdot E} \tag{1}$$

where G is the gross return per fishing unit in the particular fishery; T is the total exvessel revenue paid to all fishermen in that particular fishery; S is the percent of revenue paid as bonus payments to fishermen; P is the percent of entry permits actually used in a particular fishery; and E is the total number of entry permits outstanding.

To estimate net returns per entry permit holder, exclusive of opportunity costs of capital, the following equation was used:

$$N_1 = G - \frac{T \cdot L}{P \cdot E} - C \tag{2}$$

where N_1 is net return not including the opportunity cost of capital; L is the percent of total

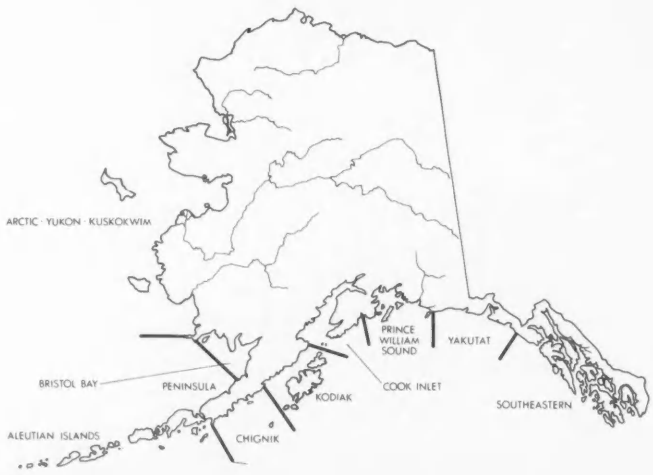

FIGURE 1.—Alaska salmon management areas.

TABLE 1.—Input data used to generate estimates of fishermen's incomes by fishery.

Fishery	Total exvessel revenue (T) in thousands[1]	Costs (C) per operating unit[2]	Crew share (L) [fraction of T paid][2]	Net earnings from other fisheries (X)[2]	Market value of investment (I)[2]	Fraction of gross return earned in other fisheries (F)[2]	Estimated fraction of permits actually (P) fished[3]	Earnings from nonfishing sources (O)[4]	Bonus payments (S) [fraction of T][2]	No. of entry permits issued (E)
Purse seine:										
Southeast	$9,750	$10,279	0.500	$7,390	$91,212	0.46	0.87	$4,155	0.196	395
Prince Wm Sound	4,385	5,804	.450	2,128	39,592	.31	.89	3,016	—	238
Cook Inlet	467	4,506	.510	2,607	33,657	.37	.61	4,343	.004	68
Kodiak	5,947	4,805	.430	—	37,902	.33	.91	4,685	.019	368
Chignik	2,541	10,213	.420	—	66,307	.18	.95	2,007	.045	80
Peninsula-Aleutians	1,603	1,627	.340	8,703	51,473	.74	.78	4,061	—	111
Drift gill net:										
Southeast	4,404	4,381	.072	2,583	27,254	.12	.74	4,012	.092	453
Prince Wm Sound	3,063	4,436	.058	879	15,642	.23	.79	1,906	.024	511
Cook Inlet	2,235	2,744	.176	589	15,254	.17	.67	2,501	.029	545
Peninsula-Aleutians	1,526	3,780	.092	1,171	23,428	.22	.83	1,925	—	155
Bristol Bay	13,933	1,879	.380	—	11,548	.12	.85	3,378	—	1,669
Set gill net:										
Yakutat	476	[5]2,930	—	—	[5]8,223	—	.82	1,632	—	150
Prince Wm Sound	119	[5]2,930	—	—	[5]8,223	—	.68	3,540	—	32
Cook Inlet	1,508	2,930	—	—	8,223	—	.71	3,874	.002	686
Kodiak	459	2,590	—	—	8,139	—	.83	1,511	.050	183
Peninsula-Aleutians	226	1,485	—	—	4,317	—	.48	318	—	77
Bristol Bay	1,248	1,021	—	—	1,758	—	.78	473	—	803
Power troll:										
Statewide	5,290	3,580	.272	2	33,002	.36	.88	3,439	.026	895

[1]Computed from landing records of the Alaska Department of Fish and Game for the years 1969–73. Adjusted by Wholesale Price Index using 1973 as a base year.
[2]Information gathered from a cost survey of Alaskan fishermen (Source: Owers 1974).
[3]Computed from landing records and license files of the Alaska Department of Fish and Game for the years 1969–72.
[4]Information gathered from a random sample of gear license holders. Reported from Internal Revenue Service in confidential format that did not reveal individual identities.
[5]No reliable data. Data from Cook Inlet used as an approximation.

exvessel revenue paid to crewmembers, exclusive of the entry permit holder; and C is expenses per vessel.

To estimate net returns to the entry permit holder, including the opportunity cost of capital, the following equation was used:

$$N_2 = N_1 - A \cdot B \cdot I \cdot (1 - F) - 2 \cdot N_1 \cdot B \quad (3)$$

where N_2 is the net return less opportunity capital costs; A is a constant term used to deflate the average value of investment; B is a constant used for the opportunity cost of capital; I is the average total value of investment per operating unit in the fishery as estimated by fishermen; and F is the percent of income received in other fisheries.

Finally, to estimate the entry permit holder's total annual income from all sources, the following equation was used:

$$Y = N_1 + X + O \quad (4)$$

where Y is total annual income; X is net earnings from other fisheries; and O is income earned from employment other than commercial fishing.

All these equations provide an estimate of the average rate of return per entry permit holder or operating unit in a particular fishery. Analysis of fish landings indicates that a large number of fishermen participate only a short period out of the total fishing time available. A study of returns in Alaska's fisheries shows there is evidence that the time an operator spends fishing is correlated with profit (Smith et al. see footnote 5). Therefore, the average rate of return discussed here is assumed to be the potential earnings of a fisherman who participates during the entire season in that particular fishery but, it is still likely that there will be some concentration of landings by top producers.

A further simplifying assumption in these equations is that the resource will be harvested at the same level of output with all the various numbers of operating units considered. Preliminary estimates provided by management biologists of the Alaska Department of Fish and Game indicate that the magnitude of cutbacks described in this paper would not affect the ability of the salmon fishing fleet to harvest at the maximum sustainable yield level (Jackman et al. 1973).

Base Period for Determining Total Exvessel Revenue

In the salmon fisheries total revenue fluctuates widely from year to year depending upon the size of the salmon runs and the price paid fishermen. In the analysis, the 5-yr period from 1969 to 1973 was used as the base period for determining the total revenue produced by the state's salmon fisheries. This period was used because it appears to be the most recent, reasonably representative period for which good data exist. The total catch value was adjusted for each year by the wholesale price index using 1973 as a base year.

It was assumed in estimating the total revenue produced by each fishery that regulatory decisions would seek to maintain an historical allocation among gear types. If a reduction in the size of the southeast drift gill net fleet were to occur, for example, it is assumed that no attempt would be made to reduce the percentage of the total catch available to this fishery. It was also assumed that gear reductions in one fishery would not be made without considering the effect on catches by other fisheries utilizing the same stock. For example, a large reduction in the Cook Inlet drift gill net fishery could lead to increased catches in the set gill net fishery if it is not reduced in some reasonable proportion.

Fixed and Variable Costs

Fishing costs include such standard items as fuel, food, repairs, moorage, administrative costs, and so forth. Average costs in each fishery were collected by means of a survey in spring 1974 (Owers 1974). For vessels fishing in several fisheries, costs were prorated among each fishery based upon the length of time fished and percent of total earnings received. Other items were specifically allocated, such as gear repairs.

Because there is presently so much excess capacity in the harvesting segment of the Alaska salmon fishery, it was assumed that the total cost of harvesting the resource was a linear function of the number of boats in the fishery. This logic is used in Equations (2), (3), and (4). While this might appear to be inconsistent with economic theory because fish production would be increased for each operating unit without increasing any factor of production, in reality it is likely that costs would decrease even faster than the number of operating units leaving the fishery. This is because overcrowding in the salmon fisheries involves frequent delays in setting nets and tangled gear, and forces operators to travel long distances to make all openings. Should substantial reductions take place in a fishery, consideration of increasing costs per boat would be necessary.

Depreciation has been standardized for all vessels to a 30-yr straight line writeoff with no salvage value. Depreciation for set net sites is standardized with a 10-yr writeoff since most equipment includes small skiffs and outboard motors with a shorter useful life span.

Labor Costs

Labor costs in the fisheries are determined by a share system and fluctuate directly in proportion to gross earnings. Crew shares are ordinarily computed before bonus payments are made to the boat operator. In the analysis, it was assumed that the entire bonus was kept by the entry permit holder, which is the logic used in Equation (2). Labor costs, as used here, do not include a return to the entry permit holder's own labor.

Capital Costs

The opportunity cost of capital is assumed to be 10% and is the constant value used in Equation (3). The estimated market value of each operating unit was used in determining capital investment in the fishing business. Average market values of vessels, equipment, and fishing gear were derived for each fishery by survey. It was found in surveys conducted by the British Columbia License Control Program that the true market value of vessels averaged about 84% of the estimated value supplied by fishermen (Campbell[6]). In this analysis it was assumed that the market value of investment was 85% of the value estimated by fishermen in the survey. This is the constant value used in Equation (3) to deflate the estimated value of investment.

In addition to vessels and gear, the capital investment in the freely transferable entry permit was included in estimating total capital costs. Theoretically the permit value might be calculated by discounting future cash flows or some

[6]Campbell, B. A. 1973. A review of the development of the buy-back program and its impact on the salmon fishery. Fish. Serv., Vancouver, B.C., 54 p.

other method of determining future benefits. The problem with this approach is that it involves making implicit assumptions about the worth of the operator's own contribution of labor and management and deducting this as an expense. As an approximation of permit value, it was assumed that the permit value would equal 2 years' net earnings for those remaining in the fishery, but further research is needed to determine actual values and the relationship between price and productivity. A preliminary survey of permit values after 6 mo of limited entry indicates permits may not be worth as much as the values used here (Anonymous 1975). Using the above relationship in Equation (3), however, the permit value will increase as the number of permits is reduced and capital costs per boat will rise.

Outside Earnings

Outside earnings come principally from two sources: earnings in other fisheries and earnings from nonfishing employment. Information on average earnings from outside employment for a randomly selected sample of gear operators who fished in 1971 and 1972 was provided by the Internal Revenue Service in a format which did not disclose individual identities (Anonymous[7]).

Data on earnings from other fisheries were extrapolated from fish price data, landing statistics, and by survey. It was assumed in the analysis that outside earnings in other fisheries would not be affected by limited entry and would remain constant, except in those instances where other fisheries produced a net loss. In those cases it was assumed that a fisherman would break even in other fisheries and the value of net earnings from other fisheries would be zero.

No data have been collected to determine how much gear operators may have earned as crewmembers in other fisheries, but it is not likely that this is a substantial amount since a fisherman responsible for a vessel in one fishery is most likely the operator in other fisheries as well. No reliable data has been collected on incomes of spouses, investment earnings, transfer payments, and pensions, so no estimates were included.

[7]Anonymous. 1975. Data collection and analysis necessary to limit entry in Alaska's salmon fisheries. U.S. Dep. Commer., NOAA, Natl. Mar. Fish. Serv., contract 03-4-208-262, Juneau, 75 p.

Fraction of Permits Issued That Are Used

Because there is no requirement that a fisherman use his entry permit every fishing season, it can be expected that not all outstanding permits will be fished.

In the analysis, the fraction of gear licenses sold to gear licenses fished during the period from 1969 to 1972 was taken as the fraction of entry permits that would be used. It will be important to monitor actual rates of participation from year to year to establish more meaningful figures.

Examples of Estimates

Using the equations and input data discussed above, tables similar to that shown in Table 2 for the southeast Alaska purse seine fishery were prepared for all those salmon fisheries which had entry limited in 1974. In each fishery, returns were first calculated using the present number of entry permits issued in that fishery. Returns were then calculated for a hypothetical reduction in the number of outstanding permits by 5% increments of the total number issued. No calculations were prepared for greater than a 45% reduction in permits because many of the assumptions discussed above would probably no longer prove correct. Table 3 shows the four estimates of returns with the present number of entry permits in each of the fisheries considered.

OPERATING UNITS NECESSARY TO ACHIEVE REASONABLE RETURNS

Once expected returns with various numbers of

TABLE 2.—Expected returns in the southeast purse seine fishery with the present number of entry permits and reductions in the number by 5% increments. No estimates have been made for greater than a 45% reduction in the number of entry permits. Similar data was prepared for all those fisheries which had entry limited in 1974.

Number of permits	Expected gross earnings	Net earnings	Net earnings less interest at 10%	Total annual income from all sources
395	$33,933	$ 9,468	$ 3,388	$21,013
375	35,719	10,507	4,219	22,052
356	37,703	11,662	5,143	23,207
336	39,921	12,953	6,175	24,498
316	42,416	14,405	7,337	25,950
296	45,244	16,050	8,653	27,595
277	48,475	17,931	10,158	29,476
257	52,204	20,101	11,894	31,646
237	56,555	22,632	13,919	34,177
217	61,696	25,624	16,313	37,169

TABLE 3.—Estimated earnings per operating unit by fishery with the present number of entry permits.

Fishery	Gross return	Net return per entry permit holder with no allowance for capital costs	Net return per entry permit holder with opportunity capital cost of 10%	Total annual income from all sources per entry permit holder
Purse seine:				
Southeastern	$33,933	$9,468	$3,388	$21,013
Prince Wm Sound	20,702	5,582	2,143	10,726
Cook Inlet	11,303	1,056	−958	8,006
Kodiak	18,096	5,655	2,365	10,340
Chignik	34,939	10,683	3,925	12,690
Peninsula-Aleutians	18,515	10,593	7,337	23,357
Drift gill net:				
Southeastern	14,346	9,019	5,177	15,614
Prince Wm Sound	7,770	2,894	1,291	5,679
Cook Inlet	6,298	2,477	905	5,567
Peninsula-Aleutians	11,862	6,990	4,039	10,086
Bristol Bay	9,821	4,210	2,504	7,588
Set gill net:				
Yakutat	3,870	940	53	2,572
Prince Wm Sound	5,469	2,539	1,332	6,079
Cook Inlet	3,102	172	−561	4,046
Kodiak	3,173	583	−225	2,094
Peninsula-Aleutians	6,115	4,630	3,337	4,948
Bristol Bay	1,993	972	628	1,445
Power troll:				
Statewide	6,820	1,432	−650	4,873

operating units have been estimated, it is possible to compare these figures with similar data from other sectors of the economy. This provides some indication of the magnitude of cutbacks in fleet size that may be necessary to achieve similar earnings in the fisheries.

Comparison With Wages Earned in a Similar Industry

As a minimum, the average rate of return should be sufficient to cover all normal operating expenses, labor costs besides those of the operator, depreciation, and a minimum return on investment of about 10%. An amount less than this indicates that the average return to the operator's labor is actually zero or less than zero. As Table 3 shows, with the present number of operating units, returns in the Cook Inlet and Kodiak set net fisheries, the Cook Inlet purse seine fishery, and the power troll fishery are not adequate. In these four fisheries, returns under this assumption were negative.

It is reasonable to expect, however, that the fisheries should provide some wage for the operator's physical labor and ability to work with mechanical equipment under hazardous working conditions. The contract construction industry is similar to the fisheries in this respect, as well as the fact that work is highly seasonal and characterized by long periods of unemployment. The comparison used here assumes that a fisherman should earn a wage equal to that of a worker in the contract construction industry during the time he is actually fishing.

The time spent in each fishery was derived by an examination of the dates of fish landings. The number of weeks shown in Table 3 represents the typical maximum length of the season between 1969 and 1972. It is recognized that not all boats fish every opening in a season, but these figures also make no allowance for the time spent preparing vessels and gear, travelling to the fishing grounds prior to the season, or time spent storing and repairing gear at the close of the season. For this reason the figures are probably somewhat conservative. Prior to the construction boom created by the Alaska pipeline, the 1973 average weekly earnings of workers in the contract construction industry in Alaska was $378 per week (Anonymous 1973b). Table 4 shows the average wage earned in the construction industry in a period of time equal to the length of the fishing season. This is compared with the number of operating units that would provide an equal rate of return to the fisherman; which can then be compared to the number of operating units now licensed.

None of the large set net fisheries or the power troll fishery are capable of earning a comparable rate of return with even a 45% reduction of entry permits. The southeast and peninsula drift gill net fisheries would require some reduction and the other drift gill net fisheries including Bristol Bay, Cook Inlet, and Prince William Sound would require substantial reductions. The purse seine

TABLE 4.—Number of permits required to produce reasonable returns assuming earnings from fishery considered are equal to wages paid in an equal time period in contract construction. The average wage in contract construction in 1973 was $378 per week.

Fishery	Length of fishing season (weeks)	Average wage paid in equal time period in contract construction	No. of permits that would provide an equal return	Present no. of permits
Purse seine:				
Southeastern	14	$5,292	356	395
Prince Wm Sound	10	3,780	202	238
Cook Inlet	10	3,780	[1]37	58
Kodiak	12	4,536	258	368
Chignik	12	4,536	76	80
Peninsula-Aleutians	12	4,536	[2]111	111
Drift gill net:				
Southeastern	22	8,316	362	453
Prince Wm Sound	19	7,182	[1]281	511
Cook Inlet	9	3,402	327	545
Peninsula-Aleutians	13	4,914	147	155
Bristol Bay	11	4,158	1,252	1,669
Set gill net:				
Yakutat	17	6,426	[1]83	150
Prince Wm Sound	9	3,402	21	32
Cook Inlet	15	5,670	[1]377	686
Kodiak	12	4,536	[1]101	183
Peninsula-Aleutians	14	5,292	54	77
Bristol Bay	9	3,402	[1]442	803
Power troll:				
Statewide	23	8,692	[1]492	895

[1]Reasonable returns cannot be achieved with a 45% reduction in entry permits.
[2]Reasonable returns can be achieved with the present number of entry permits.

fisheries, with the exception of Cook Inlet, are capable of providing a comparable rate of return with either the present maximum number or a modest reduction.

Comparison With Total Annual Earnings of Nonfarm Workers

An equally important objective of limited entry may be to bring the total income of fishermen up to levels comparable to the average earned by all workers in Alaska. It has been tacitly accepted that earnings in the fisheries, particularly in areas where few other employment opportunities exist, can be lower than in other segments of the State's economy. The continuation of this policy in the future probably makes little sense. As Alaska's economy develops, a more reasonable approach is to provide vocational training to residents of the State in areas of traditionally high unemployment so they can find employment in other sectors of the economy. If this approach is not adopted, it can be expected that job openings in the future will continue to be filled by trained persons from outside the State. In achieving increased incomes from the fisheries it should also be pointed out that a reduction in entry permits under the Alaska law will be achieved through a voluntary buy back of permits and vessels spread over as many as 10 yr. Thus, older persons in the fisheries that would have trouble finding other employment need not be displaced. Furthermore, a person who voluntarily sells to a buy-back program will receive a cash settlement that will ease the transition period.

A comparison can be made with the average incomes earned in other employment in Alaska. Estimates of total income include income from other fisheries and nonfishing employment. Because of the seasonal nature of salmon fishing, it is anticipated that many permit holders will continue to seek other employment when it is available.

Statistics collected by the Alaska Department of Labor show that average nonagricultural wage and salary earnings in 1973 were $1,006/mo, or $12,072/yr (Anonymous 1973b). Table 5 compares the number of operating units in each fishery that would be required to provide fishermen with a level of earnings equal to the state average. It is assumed that any increase in earnings will come from the particular fishery being examined.

With the exception of the small Prince William Sound set net fishery, none of the set net fisheries, the Cook Inlet and Prince William Sound drift gill net fisheries, or the power troll fishery could provide this level of income with even a 45% reduction of entry permits. The purse seine fisheries, with the exception of Cook Inlet, and the southeastern and peninsula drift gill net fisheries would provide a reasonable income with either the present number of operating units or a modest reduction.

TABLE 5.—Number of permits required to produce reasonable returns assuming the total annual income from all sources of fishermen is equal to the average earnings of nonfarm wage and salaried workers in Alaska in 1973. Nonfarm wage and salaried workers earned $12,072 in 1973.

Fishery	No. of permits required to provide total annual income of $12,072	Present no. of permits
Purse seine:		
Southeastern	[1]395	395
Prince Wm Sound	[1]214	238
Cook Inlet	41	68
Kodiak	313	368
Chignik	[1]80	80
Peninsula-Aleutians	[1]111	111
Drift gill net:		
Southeastern	[1]453	453
Prince Wm Sound	[2]281	511
Cook Inlet	[2]300	545
Peninsula-Aleutians	132	155
Bristol Bay	918	1,669
Set gill net:		
Yakutat	[2]83	150
Prince Wm Sound	19	32
Cook Inlet	[2]377	686
Kodiak	[2]101	183
Peninsula-Aleutians	[2]42	77
Bristol Bay	[2]442	803
Power troll:		
Statewide	[2]492	895

[1]Reasonable returns can be achieved with the present number of entry permits.
[2]Reasonable returns cannot be achieved with a 45% reduction in entry permits.

TABLE 6.—Number of permits required to produce reasonable returns assuming expected gross earnings equal necessary gross earnings as estimated by fishermen.

Fishery	Reasonable gross return estimated by fishermen (thousands)	No. of permits required to provide equal level of earnings	Present no. of permits
Purse seine:			
Southeastern	$31.9	[1]395	395
Prince Wm Sound	26.9	178	238
Cook Inlet	24.2	[2]37	68
Kodiak	32.8	202	368
Chignik	39.5	72	80
Peninsula-Aleutians	12.2	[1]111	111
Drift gill net:			
Southeastern	22.6	294	453
Prince Wm Sound	19.6	[2]281	511
Cook Inlet	14.5	[2]300	545
Peninsula-Aleutians	17.9	101	155
Bristol Bay	16.4	1,001	1,669
Set gill net:			
Yakutat	14.9	[2]83	150
Prince Wm Sound	14.9	[2]18	32
Cook Inlet	14.9	[2]377	686
Kodiak	11.1	[2]101	183
Peninsula-Aleutians	7.8	62	77
Bristol Bay	12.4	[2]442	803
Power troll:			
Statewide	15.3	[2]492	895

[1]Reasonable returns can be achieved with the present number of entry permits.
[2]Reasonable returns cannot be achieved with a 45% reduction in entry permits.

Comparison With Estimates Provided by Fishermen

In addition to the two measures discussed so far, as part of a survey fishermen were asked to estimate what they needed to gross from fishing in a particular year in order to earn a reasonable return (Owers 1974). In Table 6 the mean value of responses for each fishery is shown with the corresponding number of entry permits that would yield an equal level of gross earnings.

In the power troll fishery, all the set gill net fisheries with the exception of the Alaska Peninsula, the drift gill net fisheries in Prince William Sound and Cook Inlet, and the Cook Inlet purse seine fishery, it would not be possible to earn a level of earnings considered reasonable by fishermen with even a 45% reduction in entry permits.

Several other fisheries would need some reduction in the amount of gear. The purse seine fisheries in southeastern, Chignik, and the Alaska Peninsula appear capable of earning a reasonable return with either the present number of entry permits or a slight reduction.

SUMMARY BY FISHERY OF THE COMPARISONS USED

It will be noticed in Table 7 that the three comparisons used provide an estimate of the optimum number of entry permits that falls within a fairly narrow range. The following summarizes the economic performance by type of fishery.

Purse Seine

Purse seining in general appears to be the most economically viable of the four types of salmon gear fished. This is due in part to the fact that purse seiners are used in a variety of fisheries, which allows overhead expenses to be spread, and minimizes risks in any one fishery. As can be seen in Table 1, this is particularly true of the purse seine fisheries in the Alaska Peninsula and southeastern Alaska where a substantial percentage of gross earnings comes from other fisheries. The Prince William Sound and Kodiak purse seine fisheries could justify a modest reduction, although income levels would be only slightly reduced with the present maximum number. The Cook Inlet purse seine fishery, which is restricted to a hand purse seine fishery, does not appear able to provide a reasonable return with the present number of entry permits under any of the criteria.

Drift Gill Net

Unlike the purse seine fishery, the typical vessel

TABLE 7.—Number of entry permits required to produce reasonable earnings—summary of three measures.

Fishery	Return to gear operator equal to average wage in contract construction	Total annual income of gear operator equal to annual income of nonfarm wage and salaried workers	Reasonable earnings estimated by fishermen	Present no. of permits
Purse seine:				
Southeastern	356	[1]395	[1]395	395
Prince Wm Sound	202	214	178	238
Cook Inlet	[2]37	41	[2]37	68
Kodiak	258	313	202	368
Chignik	76	[1]80	72	80
Peninsula-Aleutians	[1]111	[1]111	[1]111	111
Drift gill net:				
Southeastern	362	[1]453	294	453
Prince Wm Sound	[2]281	[2]281	[2]281	511
Cook Inlet	327	[2]300	[2]300	545
Peninsula-Aleutians	147	132	101	155
Bristol Bay	1,252	918	1,001	1,669
Set gill net:				
Yakutat	[2]83	[2]83	[2]83	150
Prince Wm Sound	21	19	[2]18	32
Cook Inlet	[2]377	[2]377	[2]377	686
Kodiak	[2]101	[2]101	[2]101	183
Peninsula-Aleutians	54	[2]42	62	77
Bristol Bay	[2]442	[2]442	[2]442	803
Power troll:				
Statewide	[1]492	[2]492	[2]492	895

[1]Reasonable returns can be achieved with the present number of entry permits.
[2]Reasonable returns cannot be achieved with a 45% reduction in entry permits.

used in the drift gill net fisheries is not generally used in other fisheries besides salmon. In the southeast drift gill net fishery the present level of income appears adequate. All measures indicate that the Prince William Sound and the Cook Inlet drift gill net fisheries require a reduction in the number of entry permits. With a 45% reduction, total income and a reasonable gross income as estimated by fishermen cannot be achieved.

The Alaska Peninsula drift gill net fishery would require a reduction under all three measures examined, although substantial reductions are not required.

The Bristol Bay drift net fishery would also require a gear reduction under all of the criteria examined.

Set Gill Net

Returns in all of the set net fisheries are extremely low. The Kodiak and Cook Inlet set net fisheries cannot provide a rate of return sufficient to cover operating and capital costs. All the measures discussed indicate a 45% reduction or more. The other set net fisheries in the State would require substantial reductions in the number of entry permits.

Other data collected indicate that the set net fisheries have a rapid rate of license turnover from year to year, a high percentage of casual fishermen who participate only a few weeks out of the season, and many fishermen with low income dependence on commercial fishing (Owers 1975).

Power Troll

Returns in the power troll fishery appear inadequate to cover any of the measures discussed with a 45% reduction in permits. The fishery again cannot provide a rate of return sufficient to cover all expenses.

The power troll fishery is similar to the set net fisheries in that there is a large license turnover from year to year, and fishermen show relatively little dependence on commercial fishing for a source of income.

CONCLUSION

In many salmon fisheries it appears that restricting or reducing the number of operating units will enable earnings to rise to levels comparable to that earned in other sectors of Alaska's economy. This is probably not a practical objective in other fisheries, however, particularly the set net fisheries and the power troll fishery. This does not imply that limited entry is not necessary in these fisheries. Limited entry is still a desirable policy for management reasons and the fact that reducing or stabilizing the number of operating units in other fisheries in the same area could

result in increased catches by these fisheries if they are not limited.

Rather, the problem that must be faced is one of resource allocation. If a commercial fishery cannot be made a viable economic enterprise, the public interest to be served by allowing it to exist at all must be carefully examined. This is particularly relevant in such areas as Cook Inlet and southeastern Alaska where sport fishing is in many cases in direct competition with the commercial fisheries for a share of the resource. The fisheries are a valuable asset that belong to all the people of a state and allocation decisions must be made with this in mind.

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ABUNDANCE AND POTENTIAL YIELD OF THE ATLANTIC THREAD HERRING, *OPISTHONEMA OGLINUM*, AND ASPECTS OF ITS EARLY LIFE HISTORY IN THE EASTERN GULF OF MEXICO[1]

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ABSTRACT

Eggs and larvae of the Atlantic thread herring, *Opisthonema oglinum*, were collected in plankton surveys from 1971 to 1974 in the eastern Gulf of Mexico to determine spawning seasons, spawning areas, adult biomass, and potential yield to a fishery. Aspects of the early life history also were studied. Spawning occurred from February to September, but mostly from April through August, when surface temperatures were 22.5° to 30.3°C and surface salinities ranged from 32.4 to 36.8‰. Most spawning took place from the coastline out to the 30-m depth contour, and virtually all spawning occurred where depths were less than 50 m. The area of heaviest spawning was between latitudes 26°00′N and 28°00′N. The most reliable estimates of adult biomass were approximately 110,000 metric tons in 1971 and 370,000 metric tons in 1973. The most probable estimates of potential annual yield range from 60,300 to 120,600 metric tons. Based on the best larval mortality estimates, more than 99% mortality occurred from time of spawning until 19 days and 15.5 mm standard length in 1973, and approximately 98% mortality occurred for the same period in 1971.

The Atlantic thread herring, *Opisthonema oglinum* (Lesueur), is an underexploited clupeid fish that occurs widely in the western Atlantic from southern Brazil to the Gulf of Maine (Berry and Barrett 1963), but is mainly tropical and subtropical in its distribution (Hildebrand 1963). It is a coastal species that seldom occurs in depths greater than 90 m and is most abundant in depths less than 35 m (Klima 1971). In the Gulf of Mexico it is abundant and its fishery potential has been recognized for many years (Butler 1961; Reintjes and June 1961; Bullis and Carpenter 1968; Fuss et al. 1969; Houde 1973a). The total western Atlantic thread herring catch was 12,016 metric tons in 1974 (Food and Agriculture Organization 1975), of which 2,434 metric tons were landed by the United States. Some thread herring are landed as incidental catches by both Atlantic and Gulf of Mexico menhaden fleets (Klima 1971). Catch statistics are poor for thread herring in the Gulf of Mexico, but only 435 tons were reported in 1973 (Johnson 1974). However, 5,000 tons were landed from the eastern Gulf during a 4-mo period in 1967 when a preliminary attempt was made to establish a directed fishery. Based on school sightings and catch rates by commercial purse seiners, Bullis and Thompson (1967) roughly estimated that the total Gulf of Mexico thread herring stock might be 1×10^6 tons.

Eggs and larvae of thread herring have been described (Richards et al. 1974) and the species has been successfully reared from egg to juvenile under laboratory conditions (Richards and Palko 1969). There was no information on thread herring eggs or larvae from the eastern Gulf prior to my research. Kinnear and Fuss (1971) reported seasonal north-south migrations and distribution of thread herring in the eastern Gulf of Mexico, while Fuss et al. (1969) presented data on age, growth, maturity, and food habits of that stock. Fecundity of thread herring in the eastern Gulf was determined by Prest[3] and by Martinez (1972) for fish collected on the Florida Atlantic coast.

The objective of this research was to obtain a fishery-independent estimate of the abundance and potential yield to fisheries of thread herring in the eastern Gulf of Mexico based on annual surveys of eggs and larvae during 1971 to 1974. In addition, information was obtained on spawning seasons and areas, as well as on aspects of their early life history in the eastern Gulf.

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[3]Prest, K. W., Jr. 1971. Fundamentals of sexual maturation, spawning, and fecundity of thread herring (*Opisthonema oglinum*) in the eastern Gulf of Mexico. Unpubl. manuscr., Natl. Mar. Fish. Serv., NOAA, St. Petersburg Beach, Fla.

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METHODS

Adult biomass was determined from estimates of annual abundance of spawning products, a knowledge of the mean relative fecundity of thread herring, and an assumed sex ratio of 1:1 (Saville 1964; Ahlstrom 1968). Methods to determine thread herring egg and larval abundance, distribution, adult biomass, potential yield to a fishery, and mortality during egg and larval stages were analogous to methods reported in detail for round herring (Houde 1977a). Other details of survey design and planning also have been published (Rinkel 1974; Houde and Chitty 1976; Houde et al. 1976). Temperature and salinity data, as well as some egg and larvae data, from these surveys are stored in the National Oceanographic Data Center, Washington, D.C., under the MAFLA file.

The survey area was located on the broad continental shelf off western Florida in the eastern Gulf of Mexico, between lat. 24°45′N and 30°00′N (Figure 1). In 17 cruises (Table 1) from 1971 to 1974, plankton was collected with a 61-cm bongo net sampler fitted with 505- and 333-μm mesh nets. Most stations were over water depths from 10 to 200 m, except in 1974 when some stations as shallow as 5 m were added to the sampling plan. These shallow stations were added to determine if thread herring and scaled sardine, *Harengula jaguana*, spawning increased significantly nearshore where there had been no previous sampling. Thread herring eggs and larvae were identified using descriptions by Houde and Fore (1973) and by Richards et al. (1974).

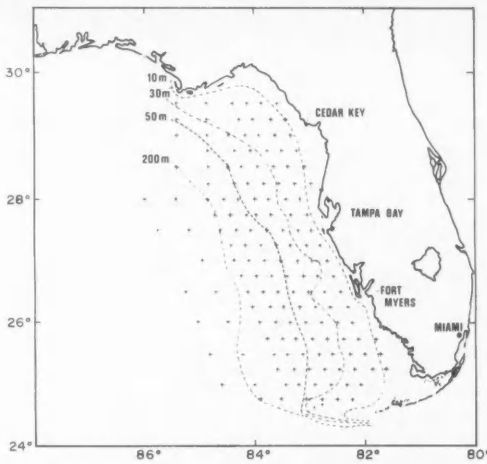

FIGURE 1.—Area encompassed by the 1971–74 eastern Gulf of Mexico ichthyoplankton surveys. Plus symbols (+) represent stations that were sampled during the survey. The 10-, 30-, 50-, and 200-m depth contours are indicated.

Egg and larval abundances at stations in the cruise area, over the time period represented by a cruise, and on an annual basis, were estimated using techniques similar to those outlined by Sette and Ahlstrom (1948), reviewed by Saville (1964), and most recently discussed by Smith and

TABLE 1.—Summarized data on cruises to the eastern Gulf of Mexico, 1971–74, to estimate abundance of thread herring eggs and larvae. GE = RV *Gerda*, 8C = RV *Dan Braman*, TI = *Tursiops*, 8B = RV *Bellows*, IS = RV *Columbus Iselin*, CL = RV *Calanus*.

Cruise	Dates	Number of stations	Positive stations for eggs[1]	Positive stations for larvae[2]	Mean egg abundance under 10 m²		Mean larvae abundance under 10 m²	
					All stations	Positive stations	All stations	Positive stations
GE7101[3]	1–8 Feb. 1971	20	0	0	0.00	—	0.00	—
8C7113								
TI7114	7–18 May 1971	123	13	47	28.42	276.82	27.67	52.63
GE7117	26 June–4 July 1971	27	4	13	0.85	14.39	17.48	51.87
8C7120								
TI7121	7–25 Aug. 1971	146	3	11	0.72	42.46	11.02	79.91
TI7131								
8B7132								
GE7127	7–16 Nov. 1971	66	0	0	0.00	—	0.00	—
8B7201								
GE7202	1–11 Feb. 1972	30	0	0	0.00	—	0.00	—
GE7208	1–10 May 1972	30	4	14	7.98	75.92	13.61	36.08
GE7210	12–18 June 1972	13	2	10	2.11	17.09	172.28	228.36
IS7205	9–17 Sept. 1972	34	0	4	0.00	—	1.04	13.78
IS7209	8–16 Nov. 1972	50	0	0	0.00	—	0.00	—
IS7303	19–27 Jan. 1973	51	0	0	0.00	—	0.00	—
IS7308	9–17 May 1973	49	4	21	60.53	999.46	34.73	101.19
IS7311	27 June–6 July 1973	51	12	19	28.28	137.98	68.74	229.37
IS7313	3–13 Aug. 1973	50	0	10	0.00	—	6.10	40.24
IS7320	6–14 Nov. 1973	51	0	0	0.00	—	0.00	—
CL7405	28 Feb–9 Mar. 1974	36	0	5	0.00	—	0.31	2.43
CL7412	1–9 May 1974	44	10	22	13.98	75.53	30.80	57.56

[1]Positive station is a station at which thread herring eggs were collected.
[2]Positive station is a station at which thread herring larvae were collected.
[3]An ICITA 1-m plankton net was used on this cruise. On all other cruises a 61-cm bongo net was used.

Richardson (in press). Variance estimates on cruise and on annual egg abundance estimates were calculated by methods used by Cushing (1957) and Taft (1960). Houde (1977a) has given detailed procedures, including estimating formulae, that were used to obtain abundance estimates of clupeid eggs and larvae in eastern Gulf of Mexico surveys.

Two methods were used to estimate adult biomass, based on two different procedures for determining annual spawning by thread herring. The first procedure is that given by Sette and Ahlstrom (1948). The estimate of annual spawning depends on integrating station and cruise estimates over area and time. The second procedure is based on a modification of Simpson's (1959) method in which annual spawning is estimated by plotting the daily spawning estimates for each cruise against the middate of the cruise and then determining the area under the resulting polygon by planimetry.

Potential Yield to a Fishery

Houde (1977a) used the estimator suggested by Alverson and Pereyra (1969) and Gulland (1971, 1972) to predict potential yield of round herring in the eastern Gulf. The same procedure was used for thread herring. The estimating formula is $C_{max} = XMB_0$ where X is assumed to equal 0.5, M is the natural mortality coefficient, and B_0 is the virgin biomass. My biomass estimates are estimates of B_0 since the thread herring stock is virtually unfished in the eastern Gulf. Because no estimate of M exists for thread herring, the potential annual yield was predicted using a range of probable values of the mortality coefficient.

Larval Abundance and Mortality

Mortality estimates were determined for larvae by length and by estimated ages. The exponential decrease in abundance of 1-mm length classes was used to calculate mortality coefficients to describe the decline in catches by length. Growth was assumed to be exponential during the larval phase. Based on this assumption and information on laboratory growth rates for thread herring larvae, ages of larvae in 1-mm length classes were estimated. Mortality coefficients were then estimated from the decline in abundance of larvae in relation to estimated age. Houde (1977a) gave estimating formulae and discussed the rationale for his procedures, which are similar to those used previously by Ahlstrom (1954) and Nakai and Hattori (1962).

RESULTS AND DISCUSSION

Occurrence of Eggs and Larvae

Thread herring eggs occurred in 8 of the 17 cruises from 1971 to 1974, and larvae occurred during 11 of the cruises (Table 1). Eggs were collected on cruises from May through August, although significant spawning may have occurred during April when no cruises were scheduled. Some larvae were collected as early as March and as late as September, but they were most abundant from May through August. No eggs or larvae were collected from September through January. Fuss et al. (1969) reported ripe or nearly ripe adult thread herring from the eastern Gulf in March through August. My data support their finding that thread herring spawning is confined to spring and summer in this area.

Most spawning takes place within 50 km of shore on the inner continental shelf in depths <30 m, and virtually all spawning occurs within 100 km of shore at depths <50 m (Figure 2). A single instance of egg occurrence beyond the 50-m depth contour was recorded (Figure 2). Spawning was most intense between lat. 26°00′N and 28°00′N, the area from just south of Fort Myers to Tampa Bay, Fla. This is the area where an attempt was made to establish a commercial fishery for thread herring in the 1960's (Fuss 1968; Fuss et al. 1969). Kinnear and Fuss (1971) found that thread herring that were concentrated near Fort Myers (lat. 26°00′N) in winter migrated north during warmer months. My egg distribution data suggest that a large part of the thread herring population remains within the Fort Myers–Tampa Bay area throughout the year.

Larval distribution was more widespread than that of eggs, presumably due to dispersal by water currents, but was generally similar to egg distribution (Figure 2). Most larvae were collected where water depths were <50 m and only six occurrences were recorded where depths were >50 m (Figures 2–6).

Thread herring eggs and larvae were relatively common in eastern Gulf ichthyoplankton. A total of 4,236 thread herring eggs were collected during the 17 cruises, 1.39% of the 304,507 total fish eggs

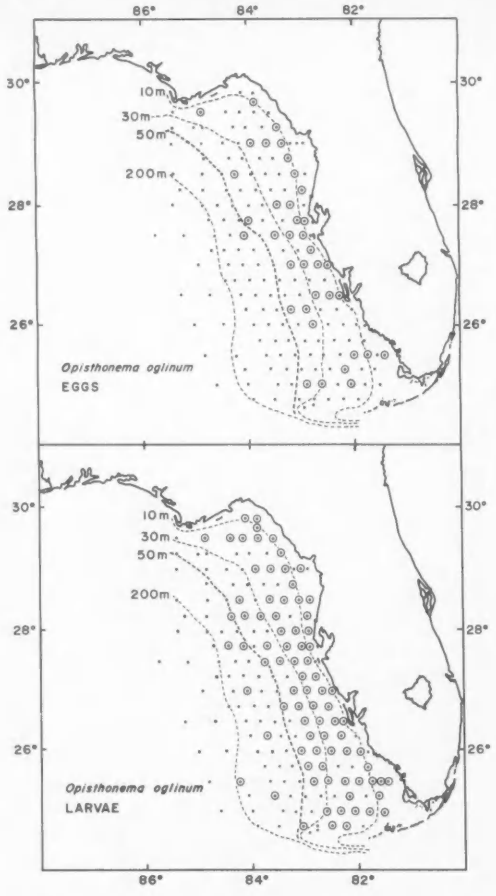

FIGURE 2.—Top. Stations in the survey area where eggs of thread herring were collected at least once during 1971–74. Stations where eggs did not occur are indicated by dots. Bottom. Stations in the survey area where larvae of thread herring were collected at least once during 1971–74. Stations where larvae did not occur are indicated by dots.

sorted from 867 samples. Number of thread herring larvae totalled 11,255, 7.87% of the 143,004 total larvae collected throughout the survey. Thread herring eggs constituted 13.20% of the total clupeid eggs collected, and thread herring larvae constituted 39.69% of the clupeid larvae.

Mean abundances of thread herring eggs under 10 m² of sea surface ranged from 0.00 to 60.53 for the 17 cruises (Table 1). At positive stations, cruise means ranged from 14.39 to 999.46 under 10 m². Most egg abundances at individual stations were <100 under 10 m² of sea surface, but abundances ranged from 101 to 1,000 under 10 m² on eight occasions and >1,000 under 10 m² on four occasions (Figures 3–6).

Thread herring larvae mean abundances for the 17 cruises ranged from 0.00 to 172.28 under 10 m² of sea surface (Table 1). At positive stations, mean cruise abundances ranged from 2.43 to 229.37 under 10 m². Larval abundances exceeded 1,000 under 10 m² on three occasions (Figures 3–6) and frequently were in the range of 101 to 1,000 under 10 m². Detailed summaries of station and cruise data for both larvae and eggs of thread herring were recently published (Houde et al. 1976).

Spawning intensity appeared to vary within the observed spawning area. The $\log_{10}$ mean egg abundance under 10 m² for positive stations from all cruises was 1.3837 at stations ≤30 m deep but was only 1.2750 at stations >30 m. The means did not differ significantly (t-test, $P>0.50$). But, the surface area encompassed by the ≤30-m depth zone was 76.03×10^9 m² as opposed to only 30.69×10^9 m² in the 30- to 50-m depth zone, beyond which virtually no spawning was observed (Figure 2). Most eggs were spawned where depth was <30 m.

There was no evidence that spawning intensity increased nearer to the coast than measured by our usual survey stations, based on cruise CL7412 (Figure 6, Table 1), when 12 nearshore stations were added to the usual stations. Thread herring eggs were collected at three of the nearshore stations and at seven of the regular, more offshore stations (Figure 6) on that cruise. The $\log_{10}$ mean catch under 10 m² was higher at the offshore stations, but due to the small number of stations it did not differ significantly ($P>0.10$) from the nearshore stations' mean:

Stations	*No. of stations with thread herring eggs*	$Log_{10}\ \bar{x}$	$Log_{10}\ S_{\bar{x}}$
Regular	7	1.5272	0.5064
Nearshore	3	0.5525	0.3101

$t_{calc} = 1.69$ $\quad t_{0.05(2,\,8)} = 2.306$

Temperature and Salinity Relations

Thread herring eggs were collected where surface temperatures ranged from 22.5° to 30.3°C and surface salinities from 32.4 to 36.8‰. From May to September temperatures from surface to 15 m were nearly homothermous, but temperatures at the 30-m depth often differed from the surface by

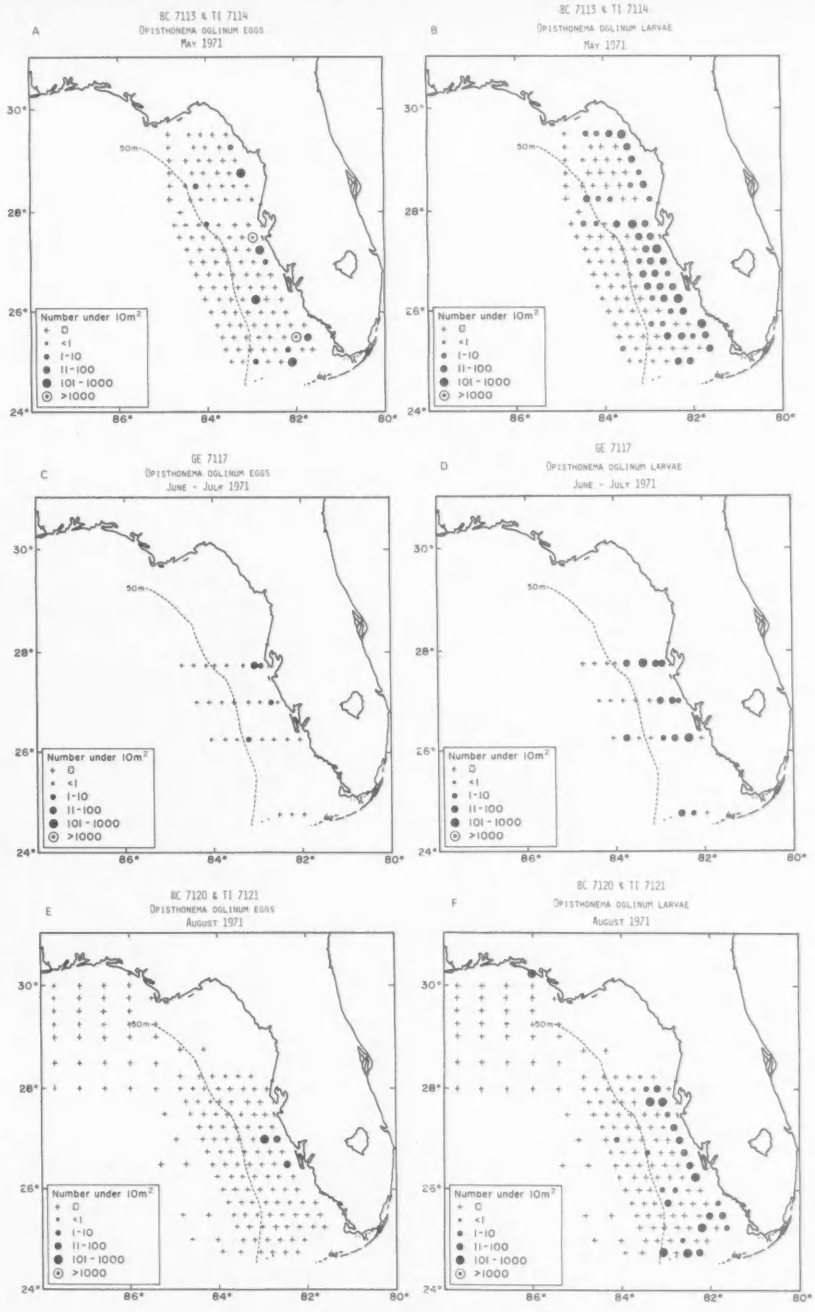

FIGURE 3.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface A, B. Cruise 8C7113–TI7114, May 1971. C, D. Cruise GE7117, June–July 1971. E, F. Cruise 8C7120–TI7121, August 1971.

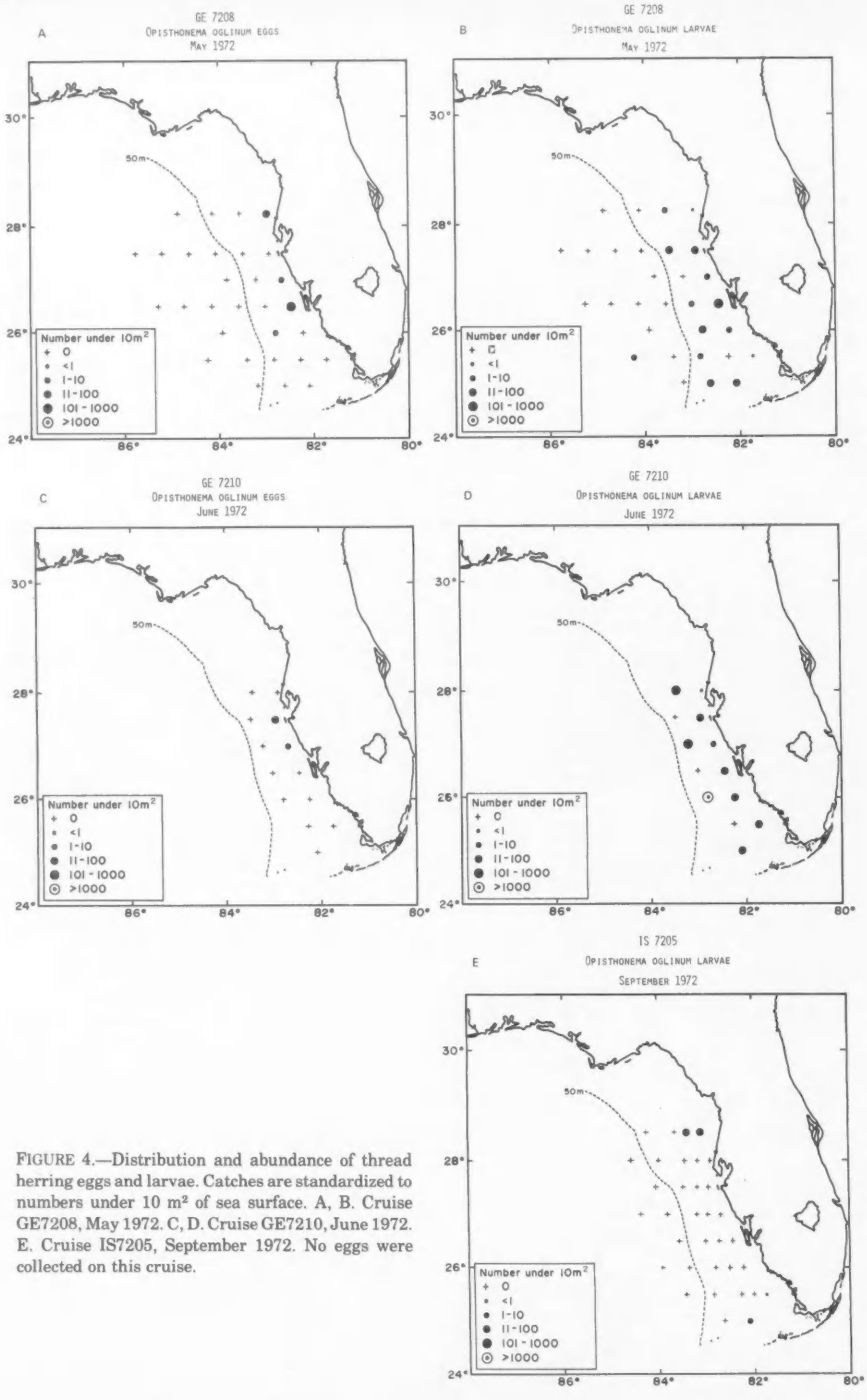

FIGURE 4.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise GE7208, May 1972. C, D. Cruise GE7210, June 1972. E. Cruise IS7205, September 1972. No eggs were collected on this cruise.

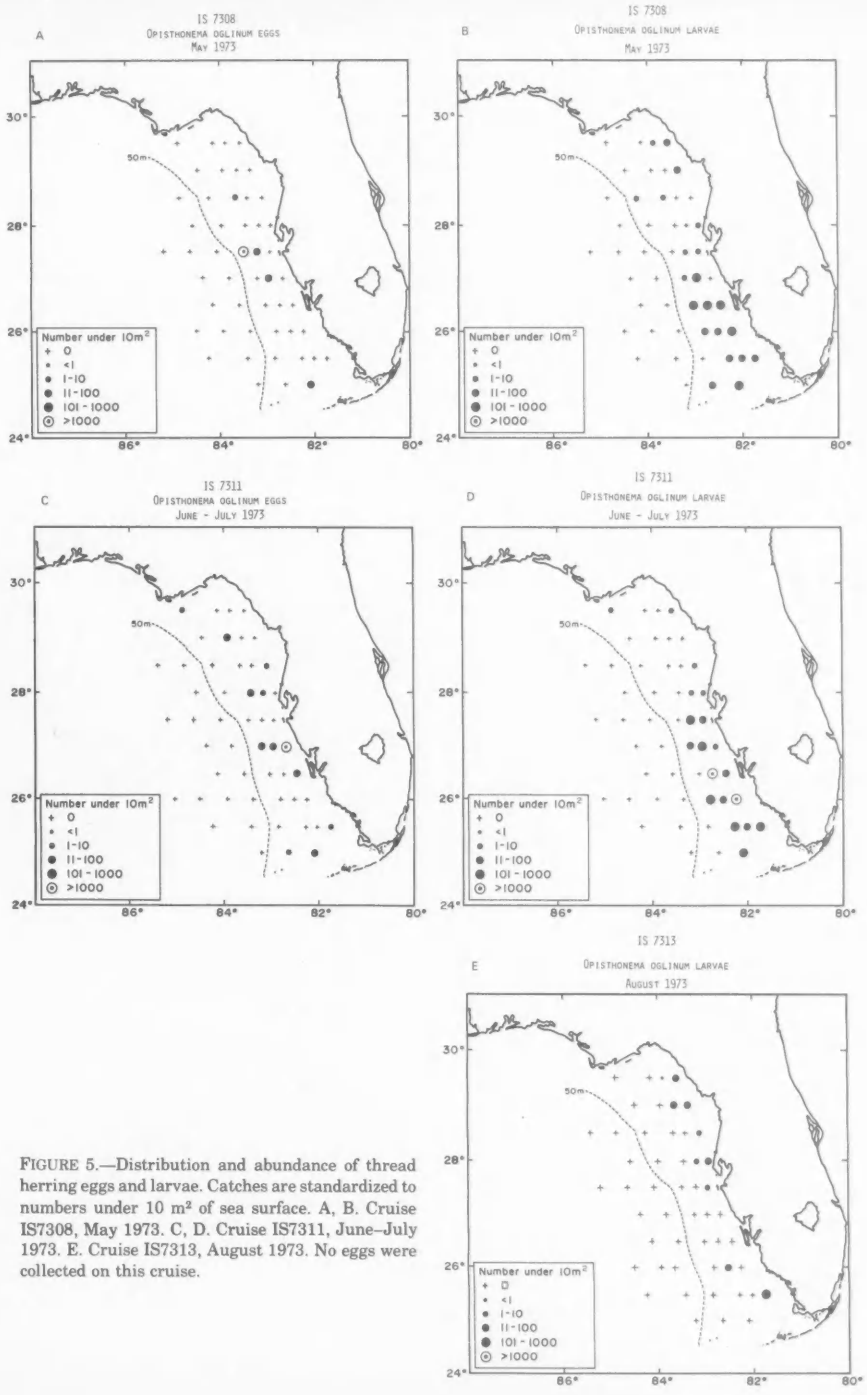

FIGURE 5.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise IS7308, May 1973. C, D. Cruise IS7311, June–July 1973. E. Cruise IS7313, August 1973. No eggs were collected on this cruise.

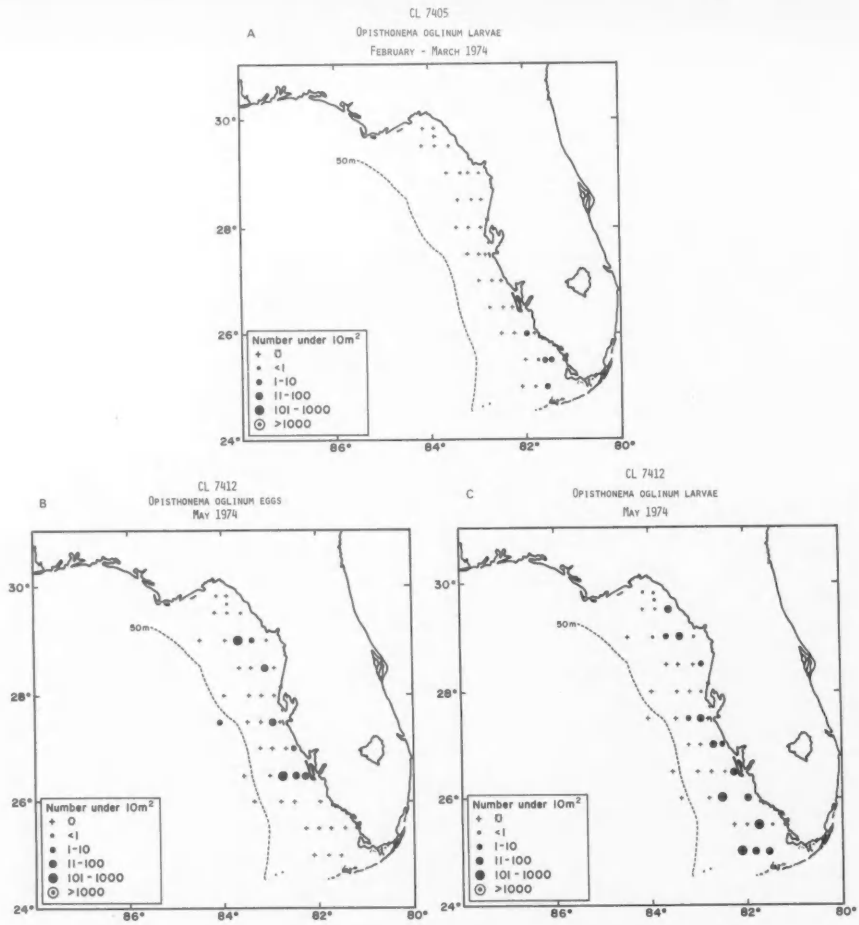

FIGURE 6.—Distribution and abundance of thread herring eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A. Cruise CL7405, February–March 1974. No eggs were collected on this cruise. B, C. Cruise CL7412, May 1974.

2° to 3°C, with a maximum difference of 5°C observed. At the 50-m depth, temperatures differed from the surface by as much as 9°C, but usually by 3° to 5°C. Because most spawning takes place at depths less than 30 m, it is unlikely that spawning and surface temperatures differed by more than 2°C. Salinity did not differ by more than 1‰ from surface to the 50-m depth, except in 1973, when surface salinities over wide areas during summer were depressed (Anonymous 1975)[4] due to Mississippi River runoff some months earlier. In 1973 salinity differences as great as 4‰ between surface and 50 m were observed in areas where some thread herring spawning occurred. Small larvae (≤5.0 mm standard length [SL]), <5 days old, were collected where surface temperatures were 18.5° to 30.9°C and salinities were 27.3 to 36.9‰. The ranges were greater for larvae than for eggs.

Based on combined 1971–74 data, most thread herring eggs and ≤5.0-mm larvae were collected at surface temperatures from 25.1° to 30.0°C (Figure 7). All stations with eggs and more than 98% of the stations with ≤5.0-mm larvae had surface temperatures above 22°C. More than 74% of the

[4]Anonymous. 1975. Compilation and summation of historical and existing physical oceanographic data from the eastern Gulf of Mexico. State Univ. Syst. Fla., Inst. Oceanogr., St. Petersburg, Fla. Final Rep. to U.S. Bur. Land Manage., Contract No. 08550-CT4-16, 97 p., 10 app.

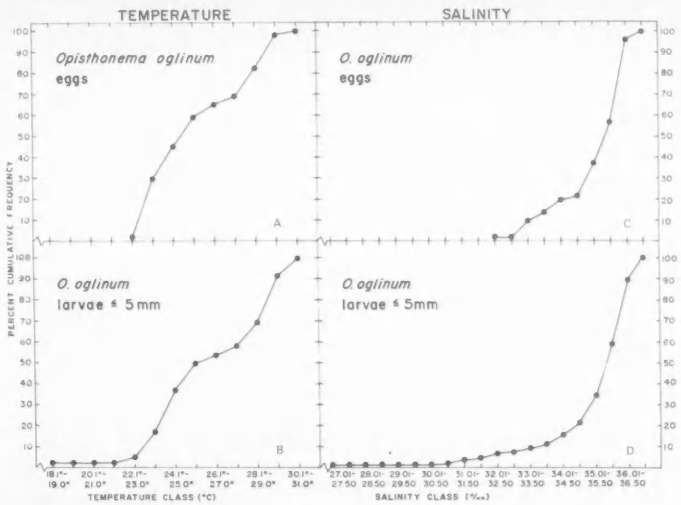

FIGURE 7.—Percent cumulative frequency distribution of 1971–74 stations where thread herring eggs occurred in relation to surface temperatures (A) and to surface salinities (C), and ≤5.0-mm SL larvae occurred in relation to surface temperatures (B) and surface salinities (D).

stations with eggs and 68% with ≤5.0-mm larvae occurred where salinity ranged from 35.0 to 36.5‰. Spawning rarely occurred at surface salinities <33‰.

Egg and Larval Abundance in Relation to Zooplankton

There was no clear relationship between abundance of thread herring eggs or larvae and zooplankton volume at stations for 12 cruises in 1972–74. Houde and Chitty (1976) determined that mean zooplankton volume from the 333-μm mesh bongo net was 153.4 cm^3/1,000 m^3 in that period. Egg abundances showed no relationship to zooplankton volumes; larvae did appear to be most abundant at stations where zooplankton volumes exceeded 153.4 cm^3/1,000 m^3. But, zero catches or low catches of larvae also were common where zooplankton volumes were high. The lack of significant correlation between larval abundance and zooplankton volume was not surprising because the 333-μm mesh does not sample zooplankton of the size eaten by small thread herring larvae.

Relative Fecundity

The mean relative fecundity of thread herring females is 594.0 ova/g ($S_{\bar{x}}$ = 29.4 ova/g), calculated from Martinez's (1972) weight and fecundity data that he obtained from nine females of 53.8 to 109.4 g. There was no apparent relationship between relative fecundity and either length or weight of the nine thread herring used in this analysis. The mean relative fecundity value was used in all subsequent biomass estimate calculations. Because mean relative fecundity with its 0.95 confidence limits is $\bar{x}$ = 594 ± 68, the maximum biomass estimating error attributable to the relative fecundity estimate is about ±11%.

Time Until Hatching

Thread herring eggs apparently hatch in <24 h at temperatures of 25° to 30°C, where most spawning takes place in the eastern Gulf. The evidence is indirect because no living thread herring eggs were available for incubation experiments. Eggs did not occur in more than one stage of development from any single sample during these surveys. Newly fertilized eggs were collected only at night, mostly from 2200 to 0200; and full-term embryos were found only during the afternoon from 1400 to 1800. I assigned a mean estimated hatching time for eggs as 0.84 days (20 h) from the evidence that was available. Thread herring eggs were rarely caught at stations sampled between the hours of 1600 and 2100, presumably because they had already hatched. Thus, abundance of thread herring eggs spawned during each cruise was underestimated. Annual spawning estimates, as well as variances, were corrected for egg stage duration (equations 4, 5; Houde 1977a) and corrected estimates were subsequently used to calculate biomasses.

Cruise Egg Abundance

The estimated abundance of thread herring eggs in the area represented by each cruise is given in Table 2. For cruises in which eggs occurred, abundances ranged from 0.86 to 91.66 × 10^{10} eggs. The Table 2 estimates, which represent abundance of eggs present on a day during a cruise, were corrected for egg stage duration and then expanded to represent the number of days encompassed by the cruise period (Sette and Ahlstrom 1948; Houde 1977a).

TABLE 2.—Abundance estimates of thread herring eggs for each cruise. Estimates were obtained using Equations (2) and (3) (Houde 1977a) and are not corrected for duration of the egg stage.

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise egg abundance (eggs × 10^{10})
GE7101	25.79	0.00	0.00
8C7113 and TI7114	120.48	55.81	34.25
G7117	101.10	48.73	0.86
8C7120 and TI7121	189.43	26.26	1.37
GE7127, 8B7132 and TI7131	72.99	0.00	0.00
8B7201 and GE7202	148.85	0.00	0.00
GE7208	124.88	65.98	11.93
GE7210	48.43	38.93	1.02
IS7205	104.59	11.16	0.00
IS7209	149.80	0.00	0.00
IS7303	149.80	0.00	0.00
IS7308	151.42	54.09	91.66
IS7311	156.50	53.21	44.26
IS7313	153.18	21.75	0.00
IS7320	153.89	0.00	0.00
CL7405	52.00	6.70	0.00
CL7412	91.33	47.89	12.77

[1]Positive area is defined as the area representing stations where either eggs or larvae of thread herring were collected.

Adjusting Cruise Egg Abundance Estimates

Because the entire potential spawning area was not sampled on cruises GE7117, 8C7120–TI7121, GE7208, and GE7210 (Figures 3, 4), an area adjustment factor was applied to correct the egg abundance estimates in Table 2. The area adjustment factor was equal to the fraction of the potential spawning area that was sampled on a given cruise. For cruise GE7117 it was 0.404; for 8C7120–TI7121, 0.746; for GE7208, 0.746; and for GE7210, 0.753. The abundance estimate for each of those cruises (Table 2) was corrected by dividing it by its area adjustment factor. Corrected abundance estimates are: GE7117—2.12 × 10^{10}; 8C7120–TI7121—1.83 × 10^{10}; GE7208—15.98 × 10^{10} GE7210—1.36 × 10^{10}.

Annual Spawning and Biomass Estimates

Method I

Estimates of total annual spawning by thread herring in the eastern Gulf ranged from 140.528 × 10^{11} eggs in 1972 to 1,105.932 × 10^{11} eggs in 1973 (Table 3). Estimated adult biomasses were 110,024 metric tons in 1971, 47,316 metric tons in 1972, and 372,367 metric tons in 1973 (Table 3). The 1972 estimate is unreliable because a cruise that was scheduled during the peak of the spawning season was terminated before completion, due to a hurricane. The actual biomass in 1972 probably is much higher than the estimate. Consider-

TABLE 3.—Annual spawning and biomass estimates for thread herring from the eastern Gulf of Mexico during 1971, 1972, and 1973 spawning seasons. Estimates are based on the Sette and Ahlstrom (1948) technique. The 1972 estimate is unreliable because a hurricane curtailed survey cruise GE7210 during the peak of the spawning season. Details of the estimating procedure are given in Houde (1977a).

Year	Cruise	Daily spawning estimate (eggs × 10^{11})	Days represented by cruise	Eggs spawned during cruise period (× 10^{11})	Variance estimates on spawned eggs (× 10^{24})	Adult biomass (metric tons)
1971	GE7101	0.000	51.5	0.000	—	
	8C7113 TI7114	4.111	74.5	306.283	20.429	
	GE7117	0.255	44.5	11.365	8.549	
	8C7120 TI7121	0.220	41.5	9.124	1.556	
Annual total				326.772	30.534	110,024
1972	8B7201 GE7202	0.000	50.0	0.000	—	
	GE7208	1.919	65.0	124.706	47.060	
	GE7210	0.163	97.0	15.822	25.507	
Annual total				140.528	72.567	47,316
1973	IS7303	0.000	46.5	0.000	—	
	IS7308	11.004	79.5	874.802	49.839	
	IS7311	5.313	43.5	231.130	20.284	
	IS7313	0.000	42.5	0.000	—	
Annual total				1,105.932	70.123	372,367

ing only 1971 and 1973 estimates of egg abundance and their respective variances, the 0.95 confidence intervals on thread herring biomass during those years ranged from 72,814 to 428,758 metric tons.

The area adjustments that corrected egg abundance estimates for four 1971 and 1972 cruises had a relatively minor effect on biomass estimates in those years. Corrected estimates, presented in Table 3, exceeded uncorrected estimates by 3,060 metric tons in 1971 and by 11,946 metric tons in 1972.

Method II

An estimate of annual spawning also was obtained by a modification of Simpson's (1959) method (Houde 1977a). Biomasses of adult thread herring were then estimated (Table 4); they were 108,139 metric tons in 1971, 45,048 metric tons in 1972, and 325,803 metric tons in 1973.

Most Probable Biomass

If the 1972 estimates are not considered, the most likely adult thread herring biomass in the eastern Gulf during 1971–73 was between 100,000 and 400,000 metric tons. Yearly fluctuations in thread herring biomass may be significant in the eastern Gulf of Mexico but the size of such fluctuations could not be determined. Severe red tides, which are common in the area, and hurricanes are just two phenomena occurring during summer months that might affect annual recruitment, causing significant year-class fluctuations. But, during the years of this study it seems unlikely that the stock of adult thread herring exceeded 430,000 metric tons and it probably was less than that amount. These estimates represent only a part of the Gulf of Mexico thread herring population. Large sotcks exist in the northern and western Gulf that are not included in the estimates. Also, juvenile thread herring biomass is not included and it may constitute a significant part of the population that could be harvested by a fishery.

TABLE 4.—Annual spawning and biomass estimates for thread herring from the eastern Gulf of Mexico during 1971, 1972, and 1973. Estimates are based on the method described by Simpson (1959). The 1972 estimate is unreliable because a hurricane curtailed survey cruise GE7210 during the peak of the spawning season.

Year	Cruise	Daily spawning estimate (eggs × 10^{11})	Annual spawning estimate (eggs × 10^{11})	Adult biomass (metric tons)
1971	GE7101	0.000		
	8C7113			
	TI7114	4.111		
	GE7117	0.255		
	8C7120			
	TI7121	0.220		
			321.172	108,139
1972	8B7201			
	GE7202	0.000		
	GE7208	1.919		
	GE7210	0.163		
			133.793	45,048
1973	IS7303	0.000		
	IS7308	11.004		
	IS7311	5.313		
	IS7313	0.000		
			967.636	325,803

Concentration of Biomass

If thread herring adults were evenly distributed from the coastline to the 50-m depth contour in 1971 and 1973, an area of 106.7 × 10^5 ha, the concentration of biomass would be in the range of 6.8 to 40.2 kg/ha, based on adult biomass estimates and the 0.95 confidence interval on those estimates. The estimated thread herring biomass concentration is less than that for round herring (Houde 1977a) which ranged from 14.1 to 102.3 kg/ha. Round herring occur in a smaller area of the eastern Gulf than thread herring; the round herring being mostly confined to the 30- to 200-m depth zone which is 76.5 × 10^5 ha. Thread herring, although less concentrated, are highly visible because of surface schooling behavior and also are presumably more accessible to a potential fishery because they are found nearer to the coast in shallower water.

Potential Yield to a Fishery

Estimates of annual potential yield of adult thread herring from the eastern Gulf range from 27,506 to 186,184 metric tons (Table 5). Estimates were obtained from $C_{max} = XMB_0$ where M, the natural mortality coefficient, was assigned three

TABLE 5.—Range of potential yield estimates for eastern Gulf of Mexico thread herring, based on biomass estimates in 1971 and 1973 by the Sette and Ahlstrom (1948) method. Yields are predicted at three possible values of M, the natural mortality coefficient. Biomass estimates were obtained from values in Table 3.

Year	Biomass estimate (metric tons)	Estimated potential annual yields (metric tons) for given values of M		
		M=0.5	M=0.75	M=1.0
1971	110,024	27,506	41,259	55,012
1973	372,367	93,092	139,638	186,184
Mean of 1971 and 1973	241,196	60,299	90,448	120,598

values (0.5, 0.75, and 1.00) within the probable range for thread herring. Based on the mean of 1971 and 1973 biomass estimates, potential yield ranged from 60,300 to 120,600 metric tons. It is likely that the sustainable yield of adult stock was in that range during 1971–73. Assuming thread herring are evenly distributed within the 106.7×10^5 ha spawning area, then probable harvestable yields of adult thread herring range from 5.6 to 11.3 kg/ha. Yield could be supplemented by some additional catch of juveniles.

The eastern Gulf thread herring stock apparently is not as large as the menhaden stock in the north-central Gulf. But, a potential harvest, based on 1971–73 biomass levels, of about 100,000 metric tons substantiates the belief that thread herring are a significant resource in the eastern Gulf that could provide raw material for the fishmeal industry. Because large fluctuations in thread herring year-class strength may occur, yield in some years could be considerably higher than that predicted based on 1971–73 abundance. The potential for thread herring harvest is higher in the eastern Gulf of Mexico than that estimated along the Atlantic coast by Pristas and Cheek (1973).

Larval Abundance

Larval abundance varied seasonally with peak abundance in spring and summer months (Table 6). Abundance estimates for cruises in which thread herring larvae were collected ranged from 0.16 to 107.57×10^{10} larvae in the survey area. Thread herring larvae were collected in small numbers on three cruises in which no eggs were taken (Table 1). Cruises IS7205 and IS7313 were made in late summer when eggs, if present, must have been rare. Larvae collected in early March, during cruise CL7405, occurred only in the southernmost part of the survey area (Figure 6). They occurred at five stations on that cruise but abundances were only 0.6 to 4.4 under 10 m². The presence of larvae indicated that some spawning began as early as February and that it continued as late as September.

TABLE 6.—Abundance estimates of thread herring larvae for each cruise. Estimates include larvae in all size classes and were obtained using Equations (2) and (3) (Houde 1977a).

Cruise	Area represented by the cruise ($m^2 \times 10^8$)	Positive area[1] ($m^2 \times 10^8$)	Cruise larvae abundance[2] (larvae $\times 10^{10}$)
GE7101	25.79	0.00	0.00
8C7113 and TI7114	120.48	55.81	33.34
GE7117	101.10	48.73	17.67
8C7120 and TI7121	189.43	26.26	20.87
GE7127, TI7131, and 8B7132	72.99	0.00	0.00
8B7201 and GE7202	148.85	0.00	0.00
GE7208	124.88	65.98	20.36
GE7210	48.43	38.93	83.43
IS7205	104.59	11.16	1.09
IS7209	149.80	0.00	0.00
IS7303	149.80	0.00	0.00
IS7308	151.42	54.09	52.58
IS7311	156.50	53.21	107.57
IS7313	153.18	21.75	9.34
IS7320	153.89	0.00	0.00
CL7405	52.00	6.70	0.16
CL7412	91.33	47.89	28.13

[1]Positive area is defined as the area representing stations where either eggs or larvae of thread herring were collected.

[2]Values are not adjusted for cruises that did not encompass the entire area, nor have estimates been corrected to account for gear avoidance by larvae at stations sampled in daylight.

The seasonal nature of thread herring larvae abundance can be observed in plotted length–frequency distributions for each cruise in which larvae were collected (Figure 8). Larvae were represented in length classes up to 23.0 mm SL, but specimens longer than 15.0 mm were uncommon. The smallest length classes (1.1–3.0 mm) represent larvae in poor condition or that were distorted from net capture and preservation, because recently hatched thread herring larvae are 3.8 to 4.0 mm SL (Richards et al. 1974).

Fewer larvae were collected at stations sampled during the day than at night, indicating that gear avoidance was relatively great during daylight, particularly by larger larvae. The ratio of night catches to day catches increased rapidly when summed catches under 10 m² over all cruises were plotted for each 1-mm length class (Figure 9). No larvae longer than 17.0 mm were collected during daylight. An exponential function $R = 0.3470e^{0.2492X}$ was fitted to the plotted data for larvae up to 17.0 mm (Figure 9), where R is the ratio of night-caught to day-caught larvae and X is standard length. It provided the correction factor R (Houde 1977a), by which daytime catches were adjusted to obtain abundance estimates of larvae by 1-mm length classes in each station area on a cruise. The correction for undersampling during daylight probably did not completely account for gear avoidance by larvae (Smith and Richardson in press), but it helped to provide a better estimate of larval abundance for subsequent estimation of survival rates. The observed increase in ratio of night- to day-caught thread herring larvae throughout the larval period seems typical of clupeid larvae (Ahlstrom 1954, 1959; Lenarz 1973; Matsuura in press). But, observations on round

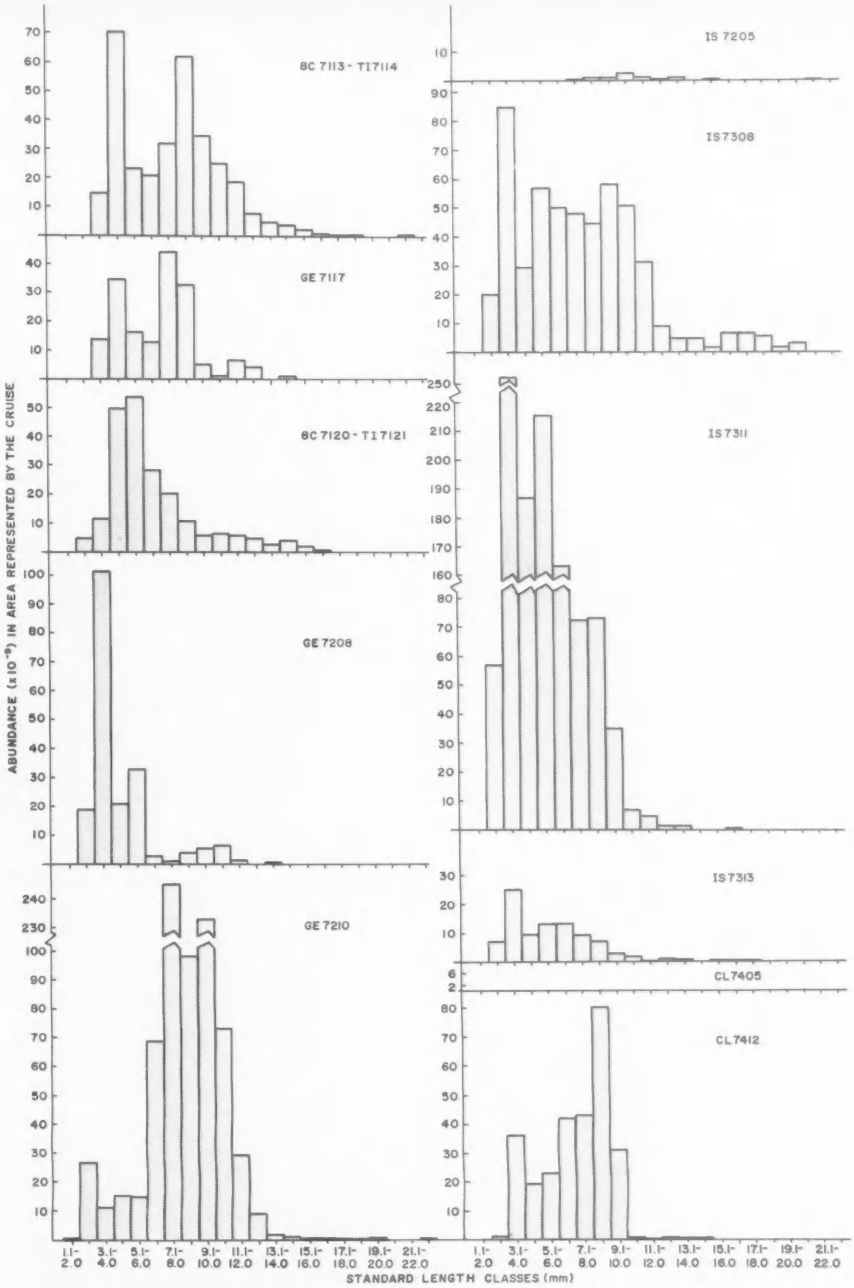

FIGURE 8.—Length–frequency distributions of thread herring larvae for 1971–74 cruises to the eastern Gulf of Mexico. Frequencies are expressed as estimated abundance of larvae in each length class within the area represented by the cruise. No adjustments for abundance have been made for cruises that did not cover the entire area where thread herring larvae might occur.

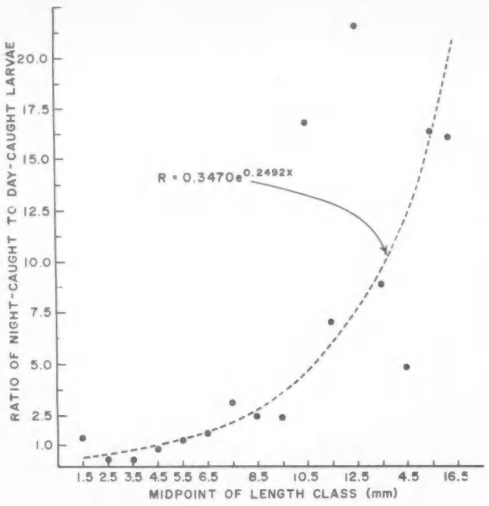

FIGURE 9.—Night to day ratios of sums of catches, standardized to numbers under 10 m^2 of sea surface, for thread herring larvae collected in 1971–74 in the eastern Gulf of Mexico. The ratios were calculated for larvae within each 1-mm length class from 1.1 to 17.0 mm SL. A fitted exponential regression describes the relationship. Larval abundance estimates for each length class at stations occupied during daylight were corrected by the appropriate ratio factor for each length class to account for daytime avoidance.

herring larvae (Houde 1977a) showed relative increases in night catches until larvae were 13.0 mm; then the ratio declined to unity for larger larvae. In scaled sardine larvae (Houde 1977b), the ratio increased throughout the larval size range, but the relative increase in night catches was slight compared to thread herring.

Annual estimates of larval abundance by 1-mm length classes were calculated for 1971 and 1973 (Figure 10), after the data had been corrected for daytime avoidance. Abundance of larvae was slightly higher in 1973 than in 1971. The abundance of 3.0- to 7.0-mm larvae accounted for the difference between the two years (Figure 10). Larvae longer than 17.0 mm were more abundant in 1973 than in 1971.

Abundance of larvae decreased exponentially in both years as lengths increased (Figure 10). Exponential functions were fitted to data in the 4.1- to 19.0-mm length classes in 1971 and to the 5.1- to 20.0-mm length classes in 1973 (Figure 10), giving estimates of the instantaneous decline in abundance of thread herring larvae per millimeter increase in length. The instantaneous coefficients estimate larval mortality rates if gear avoidance

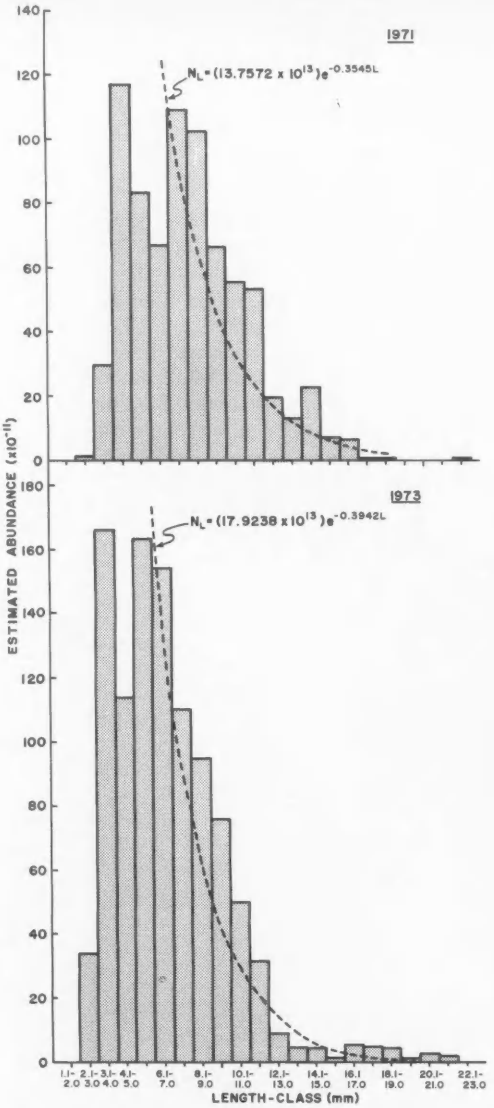

FIGURE 10.—Length–frequency distribution of annual larval abundance estimates for thread herring larvae collected in the eastern Gulf of Mexico, 1971 and 1973. Frequencies in each 1-mm length class are expressed as estimated annual abundance and have been corrected for daytime avoidance. Fitted exponential functions provide estimates of the instantaneous coefficient of decline in abundance by length.

is not too great over the length ranges in the analysis. Coefficients were $Z = 0.3545$ in 1971 and $Z = 0.3942$ in 1973. The corresponding percentage

losses per millimeter increase in length are 29.9% in 1971 and 32.6% in 1973. Confidence limits on Z at the 0.95 probability level were $Z \pm 0.0816$ in 1971 and $Z \pm 0.1385$ in 1973. The mortality coefficients did not differ significantly between years (t-test; $P>0.50$).

Mortality coefficients for round herring larvae per millimeter increase in length were $Z = 0.2269$ in 1971–72 and $Z = 0.3647$ in 1972–73 in the eastern Gulf of Mexico (Houde 1977a). Larval mortality of scaled sardines in 1973 was $Z = 0.3829$ (Houde 1977b), which is nearly identical to that for thread herring. Lenarz (1973) reported ranges of instantaneous coefficients for abundance at length data to be 0.15 to 0.33 for Pacific sardine, *Sardinops caeruleus*, and from 0.32 to 0.46 for northern anchovy, *Engraulis mordax*, larvae. The Pacific sardine coefficients were lower than those for thread herring, but the anchovy coefficients were similar to thread herring coefficients. Matsuura (in press) obtained a high instantaneous coefficient of $Z = 0.4962$ for Brazilian sardine, *Sardinella brasiliensis*, which is higher than any values observed for Gulf of Mexico clupeid larvae.

To obtain estimates of larval mortality relative to age rather than length, an exponential growth model was used to estimate age at length for thread herring larvae, given various mean daily growth increments during the larval stage. Mean daily growth increments of eastern Gulf clupeid larvae probably range from 0.3 to 1.0 mm based on laboratory rearing experiments for some species (Richards and Palko 1969; Saksena and Houde 1972; Saksena et al. 1972; Houde 1973b; Houde and Swanson 1975). At temperatures above 26°C, healthy larvae grew, on average, more than 0.5 mm/day. Duration of the egg stage for thread herring is about 0.84 days. The duration of nonfully vulnerable length classes also was estimated before mean age of each fully vulnerable 1-mm length class was calculated. Nonfully vulnerable length classes were 1.1 to 4.0 mm in 1971 and 1.1 to 5.0 mm in 1973. The duration of these stages in thread herring probably is from 1.0 to 3.0 days and 4.0 to 6.0 days, respectively, based on evidence from laboratory rearing of similar clupeid larvae (Houde et al. 1974; Houde and Swanson 1975). Eastern Gulf clupeid larvae quickly attain 4.0 mm length during the first day after hatching, but show no further growth in length until the fourth day after hatching. No direct observations of stage duration for thread herring larvae 5.0 mm or less in length were available from laboratory experiments but their growth pattern during this stage probably does not differ from that of other clupeids. Stage durations of nonfully vulnerable length classes were assigned based on observations of the other species. Methods and details of the mortality estimating procedure were given by Houde (1977a).

Two examples of duration-corrected abundance data assuming exponential growth of fully vulnerable larval length classes up to 19.0 mm in 1971 and 20.0 mm in 1973 are given in Table 7. In these examples, the mean daily growth increment was assumed to be 0.8 mm. Sets of such abundance

TABLE 7.—Two examples of data from 1971 and 1973 used to obtain stage duration, mean age, and duration-corrected abundance of thread herring eggs and larvae. Duration-corrected abundances were subsequently regressed on mean ages to obtain mortality rates (Table 8). Abundance estimates in the second column of the Table were previously corrected for daytime avoidance. In these examples, the mean daily growth increment ($\bar{b}$) was set at 0.80 mm. The nonfully vulnerable size classes were 1.1 to 4.0 mm in 1971 and 1.1 to 5.0 mm in 1973. Calculating procedures were given in Houde (1977a), Equations (12) to (16). Regressions for these data are presented in Figure 18.

Stage	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})	Stage	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})
		1971					1973		
Eggs	274.49	0.84	0.42	326.77	Eggs	921.24	0.84	0.42	1,105.93
1.1– 4.0 mm	31.65	1.00	1.34	31.65	1.1– 5.0 mm	313.69	4.00	2.84	78.42
4.1– 5.0	117.33	2.49	3.01	47.14	5.1– 6.0	163.32	2.04	5.79	80.13
5.1– 6.0	83.72	2.04	5.52	41.08	6.1– 7.0	154.18	1.73	7.88	89.33
6.1– 7.0	66.38	1.73	7.62	38.46	7.1– 8.0	109.80	1.50	9.68	73.35
7.1– 8.0	108.92	1.50	9.41	72.77	8.1– 9.0	94.93	1.32	11.25	71.84
8.1– 9.0	102.14	1.32	10.98	77.30	9.1–10.0	75.86	1.18	12.64	64.14
9.1–10.0	66.52	1.18	12.38	56.24	10.1–11.0	49.55	1.07	13.90	46.28
10.1–11.0	55.47	1.07	13.63	51.81	11.1–12.0	31.82	0.98	15.04	32.55
11.1–12.0	53.74	0.98	14.77	54.96	12.1–13.0	8.88	0.90	16.08	9.87
12.1–13.0	19.29	0.90	15.82	21.44	13.1–14.0	4.53	0.83	17.05	5.44
13.1–14.0	12.68	0.83	16.79	15.21	14.1–15.0	4.24	0.78	17.94	5.46
14.1–15.0	22.51	0.78	17.68	29.01	15.1–16.0	1.56	0.73	18.78	2.15
15.1–16.0	7.16	0.73	18.52	9.86	16.1–17.0	5.59	0.68	19.57	8.20
16.1–17.0	6.38	0.68	19.30	9.35	17.1–18.0	5.24	0.64	20.30	8.15
17.1–18.0	0.17	0.64	20.04	0.26	18.1–19.0	4.60	0.61	21.00	7.55
18.1–19.0	0.31	0.61	20.74	0.51	19.1–20.0	1.44	0.58	21.66	2.49

estimates, assigning other mean daily growth increments and other durations for nonfully vulnerable larvae, were generated. Duration-corrected abundances (Table 7) were then regressed on estimated mean ages, the resulting regression coefficients from the fitted exponential functions being estimates of the instantaneous mortality coefficients (Z) for age in days.

Examples of probable thread herring larval mortality estimates in 1971 and 1973 for a range of possible mean daily growth increments and for two probable stage durations of nonfully vulnerable larvae are given in Table 8. The ranges of probable larval mortality rates were similar in the two years. The probable instantaneous mortality coefficients ranged from 0.1371 to 0.2575 in 1971, corresponding to daily mortality rates of 12.8 to 22.7%. In 1973 the estimates of instantaneous mortality coefficients ranged from 0.1691 to 0.3050, which correspond to daily rates of 15.6 to 26.3%. The effect of varying the assumed duration of nonfully vulnerable stages had a relatively minor effect on mortality rate estimation compared with varying growth rates (Table 8).

The y-axis intercepts (N_0) of the exponential regressions used to obtain mortality estimates (Table 8) also estimate annual spawning by thread herring. The range of estimates in Table 8 encompasses the estimate obtained for 1971 and 1973 by the Sette and Ahlstrom (1948) or Simpson (1959) techniques (Tables 3, 4). At a mean daily growth increment of 0.8 mm, a probable value based on laboratory growth data, the annual spawning estimates from the y-axis intercepts (Table 8) are similar to those obtained by the other methods (Tables 3, 4).

I believe that the best estimates of larval mortality were generated from abundance and age data in Table 7. These data indicated that daily mortality of thread herring larvae was approximately 20% in both 1971 and 1973. Instantaneous mortality coefficients for conditions in Table 7 were $Z = 0.2124$ in 1971 and $Z = 0.2564$ in 1973, which correspond to daily mortality rates of 19.1 and 22.6% (Table 8). Regressions from which those instantaneous mortality coefficients were derived are given in Figure 11. Confidence intervals on Z at the 0.95 probability level ranged from 0.0990 to 0.3258 in 1971 and from 0.1993 to 0.3224 in 1973. The instantaneous coefficients were not tested to determine if they differed significantly between 1971 and 1973 because variances of the estimates were not homogeneous ($S_b^2 = 0.0028$ in 1971, $S_b^2 = 0.0007$ in 1973), but the overlapping confidence intervals indicated that they did not differ significantly.

Regressions of duration-corrected abundance on estimated mean age (Figure 11) suggested that

TABLE 8.—Summary of mortality estimates for thread herring larvae from the eastern Gulf of Mexico, 1971 and 1973. Estimates were obtained from the exponential regression of egg and larvae abundances on mean age. Instantaneous growth and mortality coefficients were calculated for various possible combinations of mean daily growth increment and duration of the nonfully vulnerable larval stages. Egg stage duration was assumed to be 0.84 days. Nonfully vulnerable larval stages were 1.1 to 4.0 mm SL in 1971 and 1.1 to 5.0 mm SL in 1973. Explanation of the estimating method is given in Equations (12) to (16) of Houde (1977a).

Year	Mean daily growth increment, $\bar{b}$ (mm)	Instantaneous growth coefficient, g	Nonfully vulnerable larvae duration (days)	Instantaneous mortality coefficient, Z	Y-axis intercept, N_0 (no. $\times 10^{11}$)	Daily mortality rate, $1 - \exp(-Z)$
1971	0.5	0.0498	1.0	0.1403	219.43	0.1309
	0.6	0.0598	1.0	0.1650	258.43	0.1521
	0.7	0.0698	1.0	0.1890	297.83	0.1722
	0.8	0.0797	1.0	0.2124	337.80	0.1913
	0.9	0.0897	1.0	0.2352	378.36	0.2096
	1.0	0.0997	1.0	0.2575	419.59	0.2270
	0.5	0.0498	3.0	0.1371	266.31	0.1281
	0.6	0.0598	3.0	0.1601	321.57	0.1479
	0.7	0.0698	3.0	0.1820	378.83	0.1664
	0.8	0.0797	3.0	0.2030	437.93	0.1837
	0.9	0.0897	3.0	0.2230	498.64	0.1999
	1.0	0.0997	3.0	0.2421	560.70	0.2150
1973	0.5	0.0498	4.0	0.1733	466.83	0.1591
	0.6	0.0598	4.0	0.2024	588.96	0.1832
	0.7	0.0698	4.0	0.2301	722.16	0.2056
	0.8	0.0797	4.0	0.2564	865.78	0.2262
	0.9	0.0897	4.0	0.2814	1,019.02	0.2453
	1.0	0.0997	4.0	0.3050	1,180.73	0.2629
	0.5	0.0498	6.0	0.1691	590.12	0.1556
	0.6	0.0598	6.0	0.1961	761.18	0.1780
	0.7	0.0698	6.0	0.2211	948.51	0.1983
	0.8	0.0797	6.0	0.2442	1,149.53	0.2167
	0.9	0.0897	6.0	0.2656	1,361.12	0.2333
	1.0	0.0997	6.0	0.2853	1,580.16	0.2482

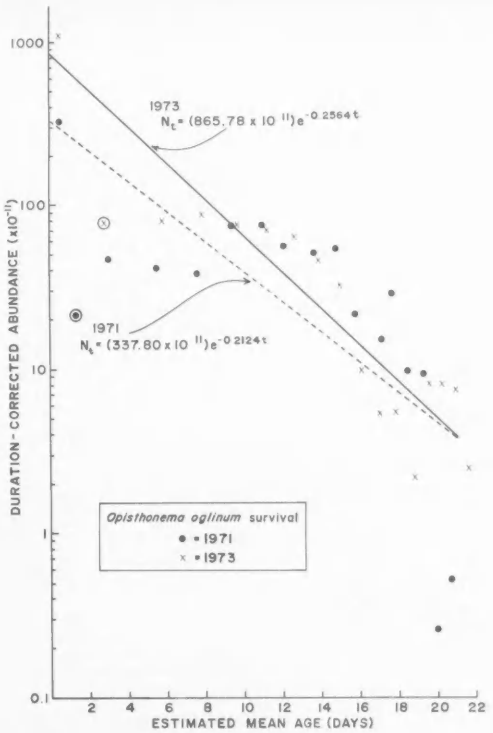

FIGURE 11.—Estimated abundance of egg and larval stages of thread herring in the eastern Gulf of Mexico in 1971 and 1973. Abundance is expressed as a function of estimated age. Fitted exponential functions give estimates of the instantaneous rates of decline in abundance for eggs and larvae up to 21 days of age. The two symbols enclosed in circles represent nonfully vulnerable length classes and were not included in the regression of instantaneous decline.

abundance of young larvae was underestimated in each year. If this is true, then mortality estimates (Table 8) are too low. Also, if growth was not exponential, but linear, then abundance of larvae in older age-classes was overestimated and mortality rates of thread herring larvae would be greater than estimates from the regression coefficients (Table 8).

Houde (1977a) estimated instantaneous mortality coefficients from abundance at age data for round herring larvae to be $Z = 0.1317$ in 1971–72 and $Z = 0.1286$ in 1972–73. These estimates are lower than the most probable rates for thread herring larvae. The estimated mortality coefficient ($Z = 0.2835$) for scaled sardine larvae in 1973 was similar to those for thread herring (Houde 1977b). The thread herring instantaneous mortality coefficients for abundance at age data were similar to those for Pacific sardine ($Z = 0.16$–0.17) (Ahlstrom 1954), jack mackerel ($Z = 0.23$) (Farris 1961), and Japanese mackerel ($Z = 0.3295$) (Watanabe 1970), but higher than those reported for Japanese sardine ($Z = 0.1279$) (Nakai and Hattori 1961) or plaice ($Z = 0.0209$ to 0.0685) (Bannister et al. 1974).

Estimated numbers and percentage survival of thread herring at hatching, 5.5 mm SL, and 15.5 mm SL were calculated given three possible instantaneous growth rates, corresponding to mean daily growth increments of 0.6, 0.8, and 1.0 mm (Table 9). The estimating procedure used parameters from the exponential functions describing decline in numbers by age (Table 8) and the age-at-length data assuming exponential growth (examples in Table 7). The estimated number of spawned eggs, from Table 3, varied by more than a factor of three between 1971 and 1973, yet the estimated number of survivors when larvae begin to transform to juveniles (15.5 mm SL) (Richards et al. 1974) was not much different between years (Table 9). Percentage survival from spawned egg to that stage did vary between 1971 and 1973; an estimated mortality of >99% occurred in 1973, but mortality was approximately

TABLE 9.—Estimated numbers and percentages of survivors of thread herring at hatching, 5.5 mm SL, and 15.5 mm SL in 1971 and 1973. Estimates are made at three possible growth rates (see Table 8). Duration of the nonfully vulnerable larval stages was set at 1.0 days for 1.1 to 4.0 mm larvae in 1971 and at 4.0 days for 1.1 to 5.0 mm larvae in 1973. The number of spawned eggs in each year was based on the estimates in Table 3. Predicted numbers at hatching, 5.5 mm, and 15.5 mm are calculated from exponential functions based on Table 8 data.

Year	Instantaneous growth coefficient, g	Number of spawned eggs ($\times 10^{11}$)	Instantaneous mortality coefficient, Z	Number hatching ($\times 10^{11}$)	Percent mortality[1] to hatching	Number of 5.5-mm larvae ($\times 10^{11}$)	Percent mortality to 5.5 mm	Number of 15.5-mm larvae ($\times 10^{11}$)	Percent mortality to 15.5 mm
1971	0.0598	326.77	0.1650	224.98	31.2	84.85	74.0	4.86	98.5
	0.0797	326.77	0.2124	282.60	13.5	104.59	68.0	6.61	98.0
	0.0997	326.77	0.2575	337.98	—	122.22	62.6	8.42	97.4
1973	0.0598	1,105.93	0.2024	496.88	55.1	171.35	84.5	5.14	99.5
	0.0797	1,105.93	0.2564	698.02	36.9	196.19	82.3	7.02	99.4
	0.0997	1,105.93	0.3050	913.87	17.4	213.98	80.7	9.00	99.2

[1]Hatching assumed to occur at 0.84 days.

98% in 1971. Estimated percentage mortalities from spawning to hatching (Table 9) were lower for thread herring than those estimated previously for round herring (35 to 90%) from the eastern Gulf (Houde 1977a). They also were lower than those (>85%) estimated for scaled sardines (Houde 1977a) in 1973. The 5.5 mm SL stage represents postyolk-sac thread herring larvae that had succeeded in starting to feed; percentage mortality to that stage was estimated to range from 62.6 to 84.5% (Table 9).

The 15.5-mm stage would be attained at 18.5 to 19.0 days if the instantaneous growth coefficient was 0.0797 (equals 0.80-mm mean daily growth increment) (Table 7). At that growth rate 20 larvae/1,000 spawned eggs would have survived to 15.5 mm SL in 1971, but only 6 larvae/1,000 eggs would have survived to 15.5 mm in 1973 (Table 9). The expected number of thread herring survivors at 15.5 mm/1,000 spawned eggs was similar to that estimated for round herring from the eastern Gulf (Houde 1977a), but greater than the number estimated for scaled sardines (Houde 1977b).

SUMMARY

1. Spawning by thread herring in the eastern Gulf of Mexico occurred from February to September, based on catches of larvae from March through September and eggs from May through August. Most spawning took place from April to August in depths <30m, within 50 km of the coast. Spawning was most intense between lat. 26°00′N and 28°00′N (Fort Myers to Tampa Bay, Fla.).

2. Eggs were collected when surface temperatures ranged from 22.5° to 30.3°C and when surface salinities were 32.4 to 36.8‰. Larvae ≤5.0 mm SL were collected at surface temperatures from 18.5° to 30.9°C and at surface salinities from 27.3 to 36.9‰. Most eggs and ≤5.0-mm larvae were taken when surface temperature exceeded 25°C and when surface salinity was above 35.0‰.

3. Estimates of adult biomass ranged from 108,000 to 372,000 metric tons in 1971 and 1973. The 0.95 confidence intervals on 1971 and 1973 estimates range from 72,800 to 428,800 metric tons.

4. The estimated concentration of adult thread herring biomass from the coast to the 50-m depth contour was in the range of 6.8 to 40.2 kg/ha. The total area in which thread herring occurred was 106.7×10^5 ha.

5. Estimates of annual potential yield to a fishery, based on 1971 and 1973 biomass estimates, ranged from 27,500 to 186,200 metric tons of adult thread herring. The potential yield, based on the mean of 1971 and 1973 biomass estimates, was between 60,300 and 120,600 metric tons.

6. Larval abundance was greater in 1973 than in 1971. Mortality rates for larval thread herring were estimated by length and for estimated ages. For lengths, the instantaneous coefficients of decline in catches were $Z = 0.3545$ in 1971 and $Z = 0.3942$ in 1973, corresponding to 29.9 and 32.6% losses per millimeter of growth. For age, the most probable daily mortality estimates were $Z = 0.2124$ in 1971 and $Z = 0.2564$ in 1973, which correspond to daily loss rates of 19.1 and 22.6%.

7. It is probable that >99% mortality occurred between spawning and the 15.5-mm stage in 1973, and that approximately 98% mortality occurred in 1971. About 20 larvae/1,000 spawned eggs were estimated to have survived to 18.5 to 19.0 days after hatching and 15.5 mm SL in 1971, but only 6 larvae/1,000 eggs were estimated to have survived to that stage in 1973.

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CHLORINATED HYDROCARBONS IN DOVER SOLE, *MICROSTOMUS PACIFICUS*: LOCAL MIGRATIONS AND FIN EROSION

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ABSTRACT

Dover sole, *Microstomus pacificus*, with and without fin erosion were collected from the municipal wastewater discharge sites of Los Angeles and Orange counties. While there was a significant difference between the total DDT levels in muscle tissue of the unaffected fish from the two regions, there was no significant regional difference between the muscle DDT levels in the diseased fish. This is consistent with the proposed hypothesis that the Orange County diseased fish had originated at the Los Angeles County discharge site. Comparisons of chlorinated hydrocarbon levels in diseased and unaffected Dover sole from the Palos Verdes discharge site of Los Angeles County indicate: 1) DDT levels were significantly higher ($P<0.05$) in Dover sole with fin erosion, and 2) polychlorinated biphenyl levels were higher at the 90% confidence level ($P<0.10$) in diseased Dover sole.

In recent years, fin erosion diseases have been observed in several species of marine fishes collected from areas contaminated by industrial or municipal waste such as the Duwamish River estuary, Wash. (Wellings et al. 1976), the New York Bight (Mahoney et al. 1973; Murchelano 1975), and major municipal wastewater discharge sites in the Southern California Bight (Mearns and Sherwood 1974). In southern California, the disease is most prevalent in the Dover sole, *Microstomus pacificus* Lockington, a marine flatfish.

Dover sole with fin erosion occur most frequently near the Palos Verdes discharge site of the Joint Water Pollution Control Plant (JWPCP) submarine outfalls of the County Sanitation Districts of Los Angeles County. During the period 1972–76, 39% of the 20,854 Dover sole collected in 268 samples off Palos Verdes had fin erosion. Only 3.5% of 894 individuals collected in Santa Monica Bay to the north (109 samples), 2.0% of 5,354 individuals collected in south San Pedro Bay to the south (138 samples), and 0.67% of 889 individuals collected off Dana Point farther south (77 samples) were affected with the disease.

The JWPCP outfalls are the dominant source of DDT residues (total DDT) and most trace metals introduced via municipal wastewaters to the Southern California Bight (Galloway 1972; Young et al. 1973; Young et al. 1976b). Although in 1974 Orange County's discharge of polychlorinated biphenyl (PCB) was twice that of any other discharger (Young et al. 1976a), the sediments off the Palos Verdes Peninsula, as a result of past discharges, have the highest levels of total PCB and total DDT found in marine sediments of the Bight (Young et al. 1976a, b).

The Dover sole is one of the most abundant and most frequently encountered species in trawl catches taken in the vicinity of the southern California submarine municipal wastewater outfalls (Southern California Coastal Water Research Project 1973). In southern California, as in northern California where it is the focus of a major bottom fishery (Hagerman 1952), Dover sole undergo seasonal onshore–offshore migrations (Mearns and Sherwood 1974). Individuals move offshore in the winter and onshore in the summer and have been collected off southern California at depths generally greater than 25 m.

In May and August 1972, trawl catches taken in the vicinity of the Orange County outfall system in south San Pedro Bay contained higher numbers of Dover sole with fin erosion than did previous catches (6 of 684 individuals and 34 of 611 individuals, respectively). This increase was associated with a large influx of Dover sole into the area. Only 273 individuals had been collected in February 1972. Orange County trawls were taken at a standard set of eight stations with the same gear and vessel combination. Only larger individuals (generally >120 mm standard length, SL) were affected with the disease; this contrasted with the situation off Palos Verdes, where Dover

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sole <120 mm SL also had eroded fins. These observations suggested that Dover sole with fin erosion caught in the vicinity of the Orange County outfall could have migrated from the Palos Verdes shelf (Mearns and Sherwood 1974). Since the increase had occurred 13 mo after the depth of discharge off Orange County had been changed from 20 to 60 m, within the range of the Dover sole, one objective of this study was to test the hypothesis that the diseased fish collected off Orange County had migrated from the Palos Verdes region and that the disease did not originate in the Orange County area. Since collections on the Palos Verdes shelf contained the highest percentage of Dover sole with fin erosion and the shelf was also the site of highest bottom sediment contamination by total DDT, we attempted to use this contamination as a tag of exposure to the JWPCP discharge area. Reported values for the biological half-life of DDT compounds in fish generally range from about 1 to 5 mo (Buhler et al. 1969; Grzenda et al. 1970; Hansen and Wilson 1970; Macek et al. 1970). Since the Orange County discharge site is about 35 km to the south of the JWPCP discharge area, it is possible that movement over this distance could occur before a significant fraction of the accumulated DDT residues had been depleted.

In Dover sole, external signs of the disease were restricted to the fins. The noninflammatory nature of the lesions and the absence of any demonstrable organisms associated with the lesions, as determined by histological examination, suggest that the disease is not the result of an infectious process (Klontz and Bendele[3]). If chemical agents are involved, then it is possible that concentrations of these agents in tissues might reflect their involvement in disease development. A second objective of this study was to explore the role of chlorinated hydrocarbons in the fin erosion disease by determining if there were differences between the levels of total DDT and total PCB in muscle tissue of Dover sole with and without eroded fins.

SAMPLING AND ANALYSIS

Fish analyzed in this study were subsamples of collections made during routine trawl monitoring surveys by the County Sanitation Districts of Los Angeles and Orange counties. During 1974, up to four trawl series were conducted off the Palos Verdes Peninsula and Orange County (Figure 1). The trawls off Orange County were conducted with a Marinovich semiballoon otter trawl with a 7.6-m (25-ft) headrope and a 1.3-cm (0.5-in) stretch mesh cod end liner. Hauls off Palos Verdes were made with a net of identical dimensions but of heavier construction and otter boards.[4] The nets were towed at a speed of 1.3 m/s (2.5 knots) and remained in contact with the ocean floor for 10 min. When the net was brought aboard ship, specimens of Dover sole, with eroded fins (diseased) and without eroded fins (unaffected), were removed, bagged, labeled, and immediately frozen. The frozen samples were returned to the laboratory and placed in freezers.

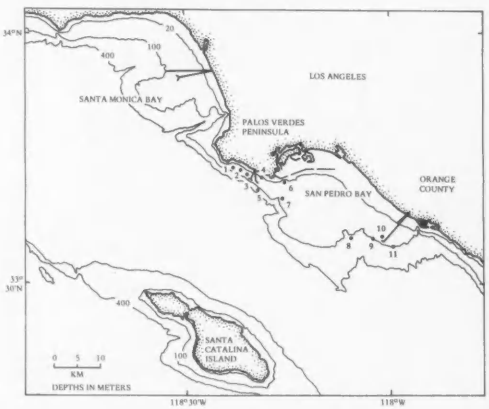

FIGURE 1.—Stations off Palos Verdes and Orange County at which Dover sole were collected.

The following numbers of Dover sole were obtained from each of the 1974 quarterly trawl series: winter (December 1973–February 1974), 10 from off Palos Verdes; spring (March–May 1974), 15 from off Palos Verdes and 5 from off Orange County; summer (June–August 1974), 6 from off Palos Verdes; and fall (September–November 1974), 17 from off Orange County.

The mean and the standard error of the standard lengths for the Palos Verdes samples with (n = 16) and without (n = 15) eroded fins were

[3]Klontz, G. W., and R. A. Bendele. 1973. Histopathological analysis of fin erosion in southern California marine fishes. South. Calif. Coastal Water Res. Proj., Rep. TM 203.

[4]This net was constructed for the Coastal Water Project by J. Willis, Morro Bay, Calif.

174 ± 3 mm and 193 ± 6 mm, respectively; the respective body weights were 78 ± 5 g and 115 ± 11 g. Measurements for the diseased (n = 14) and unaffected (n = 8) Orange County specimens were 195 ± 4 mm and 182 ± 7 mm SL, 119 ± 8 g and 98 ± 10 g, respectively. These fish were generally 3 to 4 yr old, though some were younger and some older. The mean standard lengths of several age-classes of over 425 southern California Dover sole collected at coastal locations by small otter trawl were as follows: age-class I, 70 mm; II, 140 mm; III, 170 mm; IV, 190 mm; V, 220 mm (Mearns and Harris[5]).

Muscle tissue subsamples were excised from each of the specimens when they were semi-thawed. The dissections were performed on cleaned Teflon[6] sheets, using carbon steel implements. The tissue samples were placed in glass containers, which had been heated overnight in a kiln at 538°C (1,000°F). The samples were then frozen until chemical analyses were performed.

Levels of total DDT and total PCB were measured in the samples using electron-capture gas chromatography (Young et al. 1976b). The components were identified by retention time; values were derived by comparing the peak heights of the samples with the peak heights of standards.

RESULTS AND DISCUSSION

Migration Hypothesis

The hypothesis that the diseased Dover sole collected off Orange County had migrated from the Palos Verdes shelf was tested by measuring the levels of total DDT and total PCB in muscle tissue from specimens with and without eroded fin tips from both locations. To discount possible seasonal variability, all results obtained for each disease category at an individual station were combined on a quarterly basis. To discount possible station variability, only data from those stations for which both diseased and unaffected specimens had been analyzed were used. For comparison, we used the median total DDT and total PCB concentrations for diseased and unaffected fish. Tables 1 and 2 present the results for total DDT and total PCB, respectively.

TABLE 1.—Median concentrations (milligrams per kilogram wet weight) of total DDT in muscle tissue of Dover sole, with and without eroded fins, collected off Palos Verdes Peninsula and Orange County, 1974 quarterly trawl series.

Location Station	Quarter	Diseased (with eroded fins) n	Median	Range	Unaffected (without eroded fins) n	Median	Range
Palos Verdes:							
5	Winter	3	18	15 –29	2	7.0	2.0–12
7	Winter	2	36	29 –44	3	1.8	1.3– 2.3
1	Spring	2	26	18 –34	1	25	—
2	Spring	2	20	16 –24	3	5.0	4.3– 5.3
3	Spring	3	13	7.2–45	2	11	9.6–13
4	Spring	1	16	—	1	14	—
6	Summer	3	15	8.0–29	3	11	8.8–13
Orange County:							
8	Spring	4	31	19 –75	1	7.6	—
10	Fall	6	7.6	4.2–57	2	1.0	0.3– 1.7
11	Fall	1	19	—	2	1.2	0.3– 2.2
9	Fall	3	4.2	0.9– 6.1	3	0.4	0.4– 0.5

TABLE 2.—Median concentrations (milligrams per kilogram wet weight) of total PCB in muscle tissue of Dover sole, with and without eroded fins, collected off Palos Verdes Peninsula and Orange County, 1974 quarterly trawl series.

Location Station	Quarter	Diseased (with eroded fins) n	Median	Range	Unaffected (without eroded fins) n	Median	Range
Palos Verdes:							
5	Winter	3	2.6	1.8–3.6	2	1.2	0.6–1.9
7	Winter	2	3.8	3.4–4.3	3	0.3	0.2–0.5
1	Spring	2	2.0	1.7–2.2	1	2.6	—
2	Spring	2	2.4	1.5–3.4	3	0.5	0.4–0.6
3	Spring	3	1.0	0.8–3.0	2	1.4	1.4–1.5
4	Spring	1	2.1	—	1	1.6	—
6	Summer	3	1.5	0.6–3.3	3	1.0	0.8–2.6
Orange County:							
8	Spring	4	3.0	2.1–6.6	1	0.9	—
10	Fall	6	3.4	1.3–5.2	2	4.0	1.8–6.2
11	Fall	1	1.6	—	2	0.3	0.3
9	Fall	3	0.9	0.9–1.1	3	0.3	0.2–0.3

Using the Mann–Whitney U-test, we found no significant difference ($P>0.20$) between total DDT concentrations in the muscle tissue of diseased fish from the Orange County and Palos Verdes regions. The overall median total DDT concentrations were 13 and 18 mg/kg wet weight, respectively. In contrast, there was a significant difference ($P<0.05$) between total DDT levels in the unaffected fish from the two regions (overall medians of 1.1 and 11 mg/kg wet weight, respectively).

In this study, the overall median values obtained for total DDT levels in diseased Dover sole from both areas and in the unaffected fish from Palos Verdes were 10 or more times greater than the overall median value obtained for the unaffected Orange County specimens. McDermott and Heesen (1975) had previously found that the

[5]Mearns, A. J., and L. H. Harris. 1975. Age, length, and weight relationships in southern California populations of Dover sole. South. Calif. Coastal Water Res. Proj., Rep. TM 219.

[6]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

median level of total DDT in muscle tissue from Dover sole collected off Palos Verdes was about 10 times greater than the median level observed for the Orange County specimens (McDermott and Heesen[7]).

These results support the hypothesis that the Dover sole with fin erosion collected off Orange County came from the Palos Verdes population. They also suggest that levels of DDT in tissues may be used as a tag when investigating local migrations of fish from or across a known point source of DDT.

There were no significant differences ($P>0.20$) between the total PCB levels in unaffected Dover sole from Orange County and Palos Verdes, nor between the total PCB levels in diseased fish from the two areas. The overall median total PCB concentrations in muscle tissue of unaffected fish from Orange County and Palos Verdes were 0.6 and 1.2 mg/kg wet weight, respectively; from diseased specimens, 2.3 and 2.1 mg/kg wet weight, respectively.

Association of Chlorinated Hydrocarbons with Fin Erosion

Since the diseased fish at Orange County appear to have originated from Palos Verdes and the Palos Verdes area is the primary site of total DDT and total PCB sediment contamination, only the results obtained for total chlorinated hydrocarbon measurements in diseased and unaffected Dover sole collected from Palos Verdes were utilized to test for the association of chlorinated hydrocarbons with fin erosion. Using the Mann–Whitney U-test we found that the DDT levels in diseased Palos Verdes Dover sole were significantly greater ($P<0.05$) than the DDT levels measured in unaffected Palos Verdes specimens. The overall median values for diseased and unaffected Dover sole were 18 and 11 mg/kg wet weight, respectively.

Differences in the levels of total PCB in the muscle tissue of diseased and unaffected Dover sole were significant only at the 90% confidence level ($P<0.10$). Thus there was a tendency for the total PCB levels to be higher in the diseased fish. The median values for the diseased and unaffected groups were 2.1 and 1.2 mg/kg wet weight, respectively.

These results indicate that there is a significant association between high levels of total DDT and fin erosion, and a possible association between high levels of total PCB and fin erosion in Dover sole collected off Palos Verdes.

There are several possible reasons for these associations. DDT and PCB in combination with each other and/or other constituents present in this region (such as hydrogen sulfide, high levels of trace metals, or abrasive materials) could be involved in the development of the disease. Alternatively, chlorinated hydrocarbon uptake could be enhanced in diseased fish; hence the higher levels might be the result of the disease rather than a cause. A third possibility is that the fish with fin erosion have been present on the Palos Verdes shelf longer than the unaffected fish and have been exposed to the chlorinated hydrocarbons for a longer period of time. These possible explanations are presently under investigation.

It is interesting to note that while the Palos Verdes municipal wastewater discharges of DDT significantly decreased from greater than 20 metric tons in 1971 to 2 metric tons in 1974 (Young et al. 1975), the levels of DDT in the Dover sole have remained unchanged (McDermott and Heesen see footnote 7). Similarly, the level of DDT in the surface sediments off the Palos Verdes Peninsula remained relatively constant over the 3-yr period, 1971–73 (Young et al. 1975; Young et al. 1976b). The situation for PCB is similar. The discharge of PCB decreased from greater than 19 metric tons in 1972 to 5 metric tons in 1974 (Young et al. 1976a) and the levels of PCB in the Dover sole remained unchanged (McDermott et al. 1976). Unfortunately, reliable historical data for PCB's in the Palos Verdes surface sediments are not available. The overall prevalence of fin erosion in Dover sole also remained relatively constant over the same time period (Sherwood and Mearns[8]). These findings point to the potentially significant role that the sediments may have in the uptake of chlorinated hydrocarbons and in the development of fin erosion in Dover sole.

[7]McDermott, D. J., and T. C. Heesen. 1975. DDT and PCB in Dover sole around outfalls. *In* Coastal water research project annual report, p. 117–121. South. Calif. Coastal Water Res. Proj., El Segundo.

[8]Sherwood, M. J., and A. J. Mearns. 1975. Sampling diseased fish populations. *In* Coastal water research project annual report, p. 27–32. South. Calif. Coastal Water Res. Proj., El Segundo.

SUMMARY

1. Levels of DDT in Dover sole with fin erosion collected off Palos Verdes and Orange County were not significantly different. This is consistent with the hypothesis that the Orange County diseased fish migrated from the Palos Verdes region and that the disease did not originate at Orange County.
2. A dominant point source discharge of a contaminant, such as the municipal wastewater discharge of DDT compounds off Palos Verdes, may provide a useful tag when investigating the migration of fish from or across that point source.
3. Dover sole with fin erosion from Palos Verdes have significantly higher levels of total DDT ($P<0.05$) than Dover sole without the disease from the same region.
4. There is a tendency for Dover sole with fin erosion from Palos Verdes to have higher levels of PCB ($P<0.10$) than Dover sole without the disease from the same region.

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DIEL BEHAVIOR OF THE BLUE SHARK, *PRIONACE GLAUCA*, NEAR SANTA CATALINA ISLAND, CALIFORNIA[1]

TERRY C. SCIARROTTA[2] AND DONALD R. NELSON[3]

ABSTRACT

The diel activity levels and movements of the blue shark, *Prionace glauca*, were studied in the natural environment using ultrasonic telemetry. Two initial sharks were tagged with single-channel transmitters equipped with depth sensors. Twelve sharks were tagged with multichannel transmitters with various combinations of sensors to measure depth, swimming speed, swimming direction, and temperature. From March to early June, the sharks made an evening-twilight migration from their epipelagic daytime habitat to the shallower waters bordering the island. From late June to October, the sharks remained offshore throughout the day and night. This change in movement pattern is suggested to be in response to a seasonal shift in location of prey. The telemetry data indicated that the blue shark is basically nocturnal, showing highest activity in the early evening and lowest activity in the early daylight morning. Measured parameters increasing at night included 1) rate of horizontal movement, 2) swimming speed, 3) variability in depth, and 4) variability in swimming direction. The sharks usually remained within a relatively narrow range of water temperatures.

This paper describes a study in which the diel activities of an epipelagic shark were monitored remotely in the natural environment. Multichannel ultrasonic transmitters were used to telemeter certain behavioral and environmental parameters of free-ranging blue sharks, *Prionace glauca* (Linnaeus). The primary objective was to track the sharks continuously throughout the day-night cycle to determine diel patterns of activity and movement.

Prior to the initiation of this study, surprisingly little had been published on the behavior of the blue shark, one of the most abundant large predators in warm temperate seas. Bigelow and Schroeder (1948) summarized what was then known about the biology of the species. Suda (1953) studied embryonic development, size relationsips, and sex ratios as related to distribution in the north tropical and subtropical Pacific. Strasburg (1958) investigated the distribution, abundance, capture depths, reproduction, and food habits of pelagic sharks, including the blue shark, in the central Pacific. Miscellaneous data on blue sharks have been reported from the Atlantic (Aasen 1966), the Canadian Atlantic (Templeman 1963), and the Gulf of Alaska (LeBrasseur 1964). A study of the blue shark off southern California, still largely unpublished, was conducted by Bane (1968).

More recently, the blue sharks off southwest England have received investigation in regard to age determination, reproduction, diet, and migration (Stevens 1973, 1974, 1975, 1976; Clarke and Stevens 1974). Casey, Stillwell, and Pratt at Narragansett, R.I. have gathered considerable information on the biology of sharks of that area, including data on migrations, food habits, and reproduction of blue sharks (Weeks 1974; Casey 1976; Stevens 1976). Tag returns from these studies have documented some long-range, long-term movements by blue sharks in the Atlantic. Several similar movements have also occurred in the Pacific (Bane 1968; D. R. Nelson, unpubl. data—see Discussion). Short-term movements, however, such as related to the diel cycle, have not been described for the blue shark.

Observations relating to the diel patterns of sharks have been mentioned by several authors (Springer 1963; Limbaugh 1963; Randall 1967; Hobson 1968), but specific quantitative studies have been few. Nelson and Johnson (1970) found that the horn shark, *Heterodontus francisci*, and the swell shark, *Cephaloscyllium ventriosum*, exhibited distinctly nocturnal activity patterns

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under laboratory and field conditions. In subsequent work with the horn shark, Finstad and Nelson (1975) measured the effect of light intensity on releasing activity onset, both in the natural environment and in the laboratory under artificial twilight transitions. For a colony of captive bonnethead shark, *Sphyrna tiburo*, under semi-natural conditions, Myrberg and Gruber (1974) reported a late-afternoon peak in patrolling speed, suggesting a diurnal activity rhythm.

Using ultrasonic telemetry, Standora (1972) established a basically nocturnal pattern of activity and a limited home range for the Pacific angel shark, *Squatina californica*. His multichannel transmitters were a similar, but earlier version of those used in the present study. Carey and Lawson (1973) tracked a free-ranging dusky shark, *Carcharhinus obscurus*, in order to study body temperature regulation. They used a two-channel, frequency-shifting transmitter that measured both surface and deep body temperatures. Thorson (1971) monitored long-term movements of the bull shark, *C. leucas*, with relatively long-life, sensorless pingers and automatic-recording receivers at several locations. Using this technique in conjunction with conventional tagging, he showed that bull sharks move via the San Juan River from the Caribbean Sea to Lake Nicaragua.

The present paucity of behavioral information on active, wide-ranging sharks, especially pelagic species, is undoubtedly due in part to the difficulty of studying them by direct observation. Ultrasonic telemetry now offers one promising avenue of approach to this problem. This paper reports on an initial study using this technique to investigate diel patterns of behavior in a wide-ranging pelagic shark.

METHODS

The present study is based on 14 individual telemetry trackings conducted between 3 March and 7 October 1972 (Table 1). Each tracking was initiated in the pelagic environment of the San Pedro Channel approximately 6 to 7 km north of the Isthmus, Santa Catalina Island, Calif. The blue shark was well suited for this telemetry study because of its moderately large size, high abundance for most of the year, and attractability to bait. The abundance and/or attractability of blue sharks in the offshore baiting area was low only during the months of January and February, the sharks being easily obtainable the rest of the year.

TABLE 1.—Summary of tracking data for 14 telemetered blue sharks.

Tracking no.	Date (1972)	Estimated TL (m)	Sex	Tracking duration (h)	Tracking period	Evening shoreward movement
1	3/3	1.8	M	7.0	1040–1740	?
2	3/11	2.3	F	8.5	0910–1740	?
3	3/17	2.3	?	6.4	1105–1730	beginning
4	3/30	2.0	M	11.6	1125–2300	yes
5	4/7	2.6	M	8.4	1145–2010	yes
6	4/15	2.0	F	16.1	1155–0400	yes
7	4/29	1.8	F	18.0	1200–0600	yes
8	5/6	2.0	M	21.9	1010–0805	yes
9	5/20	2.0	F	19.6	1155–0730	yes
10	6/3	2.2	M	16.3	1615–0830	yes
11	6/14	2.3	M	4.8	1145–1630	?
12	6/24	2.3	M	14.8	1445–0530	no
13	9/13	2.0	F	13.4	1305–0230	no
14	10/7	2.0	F	18.8	1215–0700	no

The estimated range in total lengths of blue sharks telemetered was 1.8 to 2.6 m; for those otherwise observed, 1.2 to 3.0 m.

Telemetry System

The ultrasonic telemetry system used in the present study has been described in detail by Standora (1972), Ferrel et al. (1974), and Nelson (1974). The transmitters were of the oil-filled type, about 15 to 18 cm long, 3.5 cm in diameter, and emitted 10-ms pulses (tone bursts) at 40 kHz. The units were set for a life of several days, and a maximum range of 3 km (average conditions) to 5 km (ideal conditions). Data were encoded as pulse rate (pulse interval) which varied with the value of resistive sensors. The first two trackings utilized single-channel transmitters incorporating depth sensors. The remaining 12 trackings were performed with multichannel units (rapid-multiplexing type) with various combinations of sensors to measure depth, swimming speed, swimming direction, and temperature.

Two commercial tunable ultrasonic receivers were used. For continuous monitoring of relatively clear, nearby signals, the Smith–Root Ta-25[4] receiver (25–80 kHz) was employed using an omnidirectional hydrophone on a 25-m cable. The more sensitive, narrow-band DuKane model N15A235 receiver (30–45 kHz) with its staff-mounted directional hydrophone was used for directional tracking and for reception of weaker signals.

[4]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

Application, Tracking, and Recovery

The sharks to be tagged were attracted with bait to the 7-m tracking boat. Cut Pacific mackerel, *Scomber japonicus*, in two bait cannisters, was suspended at depths of about 5 and 15 m. Since drifting of the boat established the odor corridor necessary for shark attraction, the time needed for attraction decreased as the wind (and drift rate) increased. The time necessary to attract the first blue shark ranged from 10 min to 4 h and the mean was 1.5 h.

Whenever a choice was possible, a larger individual shark was selected for tagging in order to lessen the possible effect of the transmitter on its behavior. The shark to be tagged was enticed to the surface next to the boat using a short baited line, then harpoon tagged in the middorsal region anterior to the first dorsal fin. The sex of the shark was noted and its total length estimated (Table 1). An attempt was made to prevent the shark from actually taking the bait, as this might have influenced subsequent feeding motivation.

The transmitter was attached to the shark by a stainless steel dart (Floy FH 69) thrust beneath the skin with a hand-held applicator pole. The transmitter package included a syntactic foam float and a magnesium breakaway link which corroded through in a roughly predictable time, allowing the unit to float to the surface for recovery.

The tracking procedure involved continuous monitoring of the signal from the drifting boat using the omnidirectional hydrophone. As the signal became weak, its direction was determined with the directional hydrophone, and the boat was then moved closer to the shark. Distance to the shark was estimated primarily from approximate signal strength and by triangulation from successive positions of the moving boat. To minimize the effect of the boat on the shark's behavior, an effort was made to maintain a distance of at least 200 m between the boat and the shark.

Ultrasonic tracking in the study area at times presented certain problems. Noise from crustaceans, echo-locating cetaceans, ship traffic, wave action, hydrophone turbulence, and bottom echoes could be picked up by the receivers, and if of high enough level, would mask the data pulses. Signal reception was also affected when the shark went below the thermocline (reflection) or was swimming very near the surface (wave shielding, bubble attenuation, downward ray refraction). These factors at times caused signal losses that could be counteracted only by lowering the hydrophone to a depth of about 10 or 15 m.

Data Recording and Reduction

Approximately once per half-hour, a 30-s data sequence was recorded on magnetic tape and the estimated position of the shark plotted. The omnidirectional hydrophone was preferred for recording purposes whenever the signal was sufficiently strong. It was less convenient to use the directional hydrophone for recording long data sequences because of the difficulty of maintaining continuous accurate aim, thus resulting in greater signal-strength variability.

Decoding of the single-channel depth data required only a stopwatch and calibration graph. Ten pulse intervals were timed and converted to a depth value. For the multichannel data, the tape recordings were converted into paper oscillograms on which the pulse intervals were measured manually. For analysis, the mean value for three clear 8-channel sequences were graphed for each half-hour recording period.

RESULTS

The telemetered blue sharks were generally most active at night, with highest activity in the early evening and lowest activity in the early daylight morning. While some activity occurred throughout the diel cycle, the mean recorded values for all trackings were greater at night for 1) rate of horizontal movement, 2) swimming speed, 3) variability in depth, and 4) variability in swimming direction. Experienced tracking personnel were also able to detect by ear subtle changes in the multiplexed pulse intervals. Although not quantified, the trackers received the distinct impression that these changes occurred more often at night—thus further supporting a nocturnal activity maximum.

Horizontal Movement—Island-Oriented Migration

The most striking behavior demonstrated by the present study was a seasonal, evening-twilight migration from the epipelagic offshore habitat to the shallower waters bordering the island. Between late March and early June, each of the seven sharks tracked made this movement to-

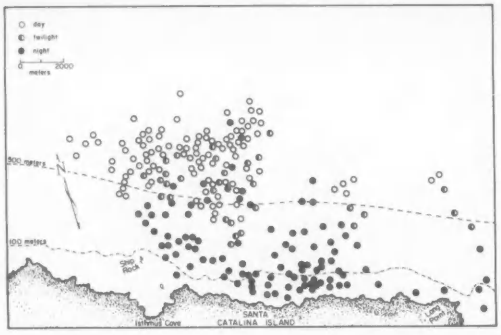

FIGURE 1.—Positions of seven blue sharks tracked from late March through early June 1972. Note that all day positions are offshore from the island, while the majority of night positions are nearshore, often in relatively shallow water.

wards the island shoreline. Examples of trackings of this type are shown in Figures 1 and 2.

These sharks remained offshore in the general vicinity of the tagging during the daylight hours. Approximately at dusk, the sharks initiated a relatively straight-line course towards the island. It is difficult to place precise times on when the sharks began this move, but it appeared to be from about 1.6 h before to 1.3 h after sunset, with a mean slightly after sunset. During the shoreward movement, the sharks swam at depths varying from near the surface to over 90 m. Once near the island, the sharks usually moved in an easterly direction parallel to the shoreline. Several hours before sunrise, there was a directed movement away from the island back to the offshore environment. The closest estimated nighttime approaches to the island for these individuals averaged 1,100 m (range, 200–4,000), corresponding to water depth averaging 115 m (range, 80–380).

Although three preliminary trackings in early and mid-March ended prior to nightfall, the last of these appeared to show the beginnings of a shoreward movement prior to transmitter release. One tracking in mid-June ended prematurely prior to dusk. From late June until early October, the three sharks successfully tracked remained offshore throughout the day and night over bottom depths of 500 m or more (Figures 3, 4).

Rate of Horizontal Movement

Rate of movement was calculated for each shark from its half-hourly estimated positions such as shown in Figures 2 and 4. The mean values for all sharks tracked (Figure 5) showed an increase in rate of movement at sunset which continued through most of the night. The mean rate of movement for the daytime was 1.2 km/h (range, 0.3–7.0); for the nighttime, 1.8 km/h (range, 0.4–4.0).

Swimming Speed

There was a definite increase in telemetered instantaneous swimming speed at night (Figure 5). However, no abrupt increase in speed occurred at the dusk transition, as might be expected in view of the rate of movement increase at that time. Swimming speed peaked a few hours after sunset and remained comparatively high until a few hours before sunrise. The artifactual burst of speed immediately after tag application was short lived, even in those sharks that did not promptly return to the bait cannister.

Although the maximum speed capability of the sensor was 5 km/h, this speed was not often reached during the half-hourly data recording periods, which suggests speeds in excess of 5 km/h seldom occurred. The mean swimming speed for the daytime was 1.3 km/h, for the nighttime 2.8 km/h, while the range for both covered the entire sensor range.

Increases in swimming speed were often associated with brief dives during the same recording session (Figures 2, 4). In seven of the eight trackings in which both speed and depth were telemetered, and where tracking extended at least into dusk, the highest mean speeds occurred at relatively great depths (means: 4.8 km/h, 69 m) while the lowest speeds occurred at much shallower depths (means: 0.5 km/h, 20 m). This suggests that some factor in deeper water stimulated this speed increase, possibly presence of food.

Swimming Direction

Figure 5 shows clearly the relationship between swimming speed and rate of movement throughout the diel cycle. As expected, swimming speeds had the higher values, as the two measures would have been equal only in cases where the shark swam in a straight line for the entire 30-min interval between position determinations. During daylight hours both rates were moderately close, suggesting that the sharks made gradual changes in swimming direction rather than abrupt

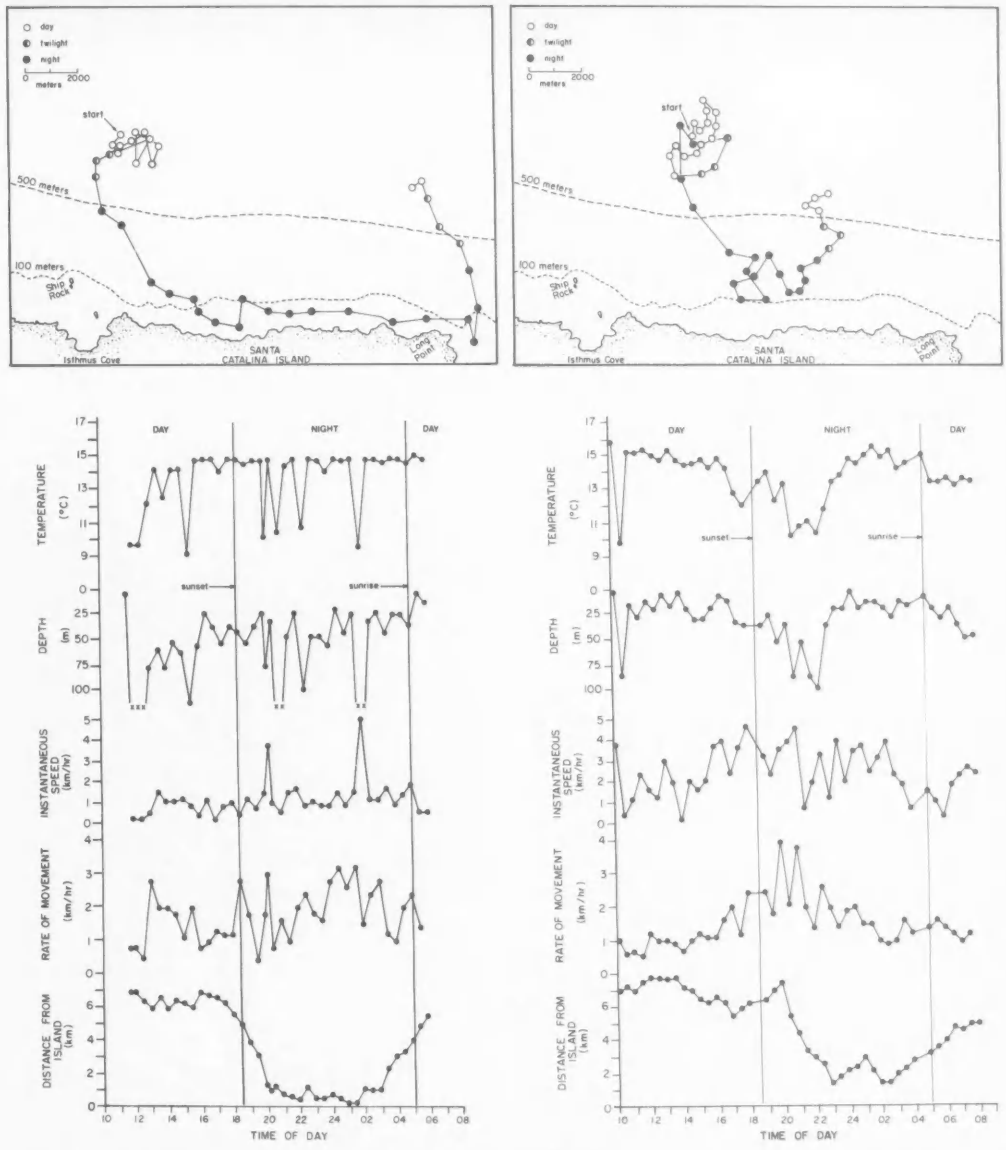

FIGURE 2.—Data from two individual trackings of blue sharks typical of the late March to early June period. Top, shark positions at approximately 0.5-h intervals. Bottom, telemetered sensor data. Note the characteristic evening-twilight migration towards the island, the initial plunge occurring immediately after transmitter application, and the close correlation between temperature and depth. Depths in excess of 110 m (the sensor limit) are indicated by ××.

changes. During the dusk transition, rate of movement most closely matched swimming speed, indicating the greatest consistency in swimming direction. In timing, this coincides with the relatively oriented shoreward migrations of from late March to early June. The greatest disparity be-

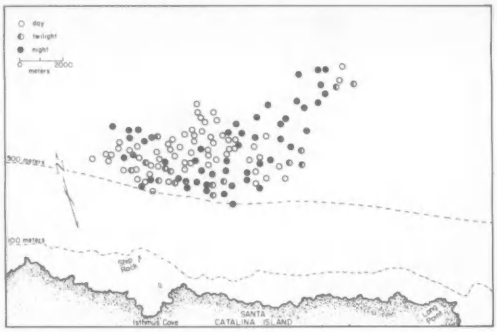

FIGURE 3.—Positions of three blue sharks tracked from late June to early October 1972. Note that both day and night positions are well offshore over relatively great depths.

tween rate of movement and swimming speed was during the early evening, evidence that much of the swimming then was variable in direction—a possible indication of searching for and/or pursuing prey. Beginning in the early morning and continuing through dawn, the differences between the two rates lessened.

A compass sensor for direct measurement of instantaneous swimming direction (azimuth) was incorporated during only one successful tracking. The compass data from this tracking (Figure 4) show that the greatest number of multiple-direction recordings (i.e., during single-recording periods) occurred at night, suggesting that variability of swimming direction is generally greater at night. During one nighttime recording, a change of at least 360° coupled with a speed change of 1 to 5 km/h was noted during one 15-s period.

Vertical Movement

Figure 6 illustrates the mean depths telemetered from all sharks with transmitters equipped with depth sensors. The sharks were within a depth range of 18 to 42 m for 92% of the time; they appeared to equal or exceed 100 m only during 3.9% of the readings (excluding initial plunges). The apparent tendency was a slight increase in mean depth at night. The mean daytime depth was 30 m; at night 40 m. Individual tracking graphs show that the sharks covered the entire depth range of the sensors (0–110 m) during both day and night, but that at night there were more vertical excursions from shallow to deep, i.e., greater variability in depth. During four trackings, the sharks may have been close to the bottom when in the relatively shallow water near the island.

The first hour of depth data were excluded from Figure 6 because of what appears to be an initial plunge induced by tagging trauma. As shown in Figure 7, the data also suggest that this initial effect decreased or disappeared within 1.5 h after tagging. About half of the sharks tagged exhibited this "abnormal" plunge (to a mean depth of at least 95 m) within 0.5 h of being tagged. The others apparently did not—possibly a result of the tag dart penetrating in a less sensitive spot. Of the first nine sharks tagged, six were seen to return to the bait cannister within seconds after transmitter application—suggesting little, if any, tagging trauma. Two of these six sharks, however, still made a deep dive by the next recording session.

Temperature

Blue sharks in the study area appeared to prefer a relatively narrow range of water temperatures. Overall, the telemetered sharks were found in a temperature range of 8.5° to 17.5°C, but occurred in the much narrower range of 14.0° to 16.0°C for 73% of the time. Seasonality of diel depth/temperature selectivity was not apparent from either the temperature or depth data. As expected, the telemetered depth and temperature data usually corresponded quite well, i.e., an increase in depth accompanied by a decrease in temperature (Figures 2, 4). Individuals were most often seen swimming at the surface during the cooler months, but rarely during either the coldest or warmest months, a behavior that may have been influenced by surface temperatures.

DISCUSSION

It is not surprising that the blue shark appears more active at night than during the day. Carcharhinids in general are considered by Randall (1967) to be nocturnal. In addition, most sharks studied quantitatively in this regard have proven to be basically nocturnal, the bonnethead shark studied by Myrberg and Gruber (1974) being a possible exception. Like other nocturnal sharks, however, blue sharks certainly feed diurnally at times, and it is common knowledge that they readily respond to opportunistic feeding stimuli (e.g., bait) during the day. There have also been observations of blue sharks feeding naturally during

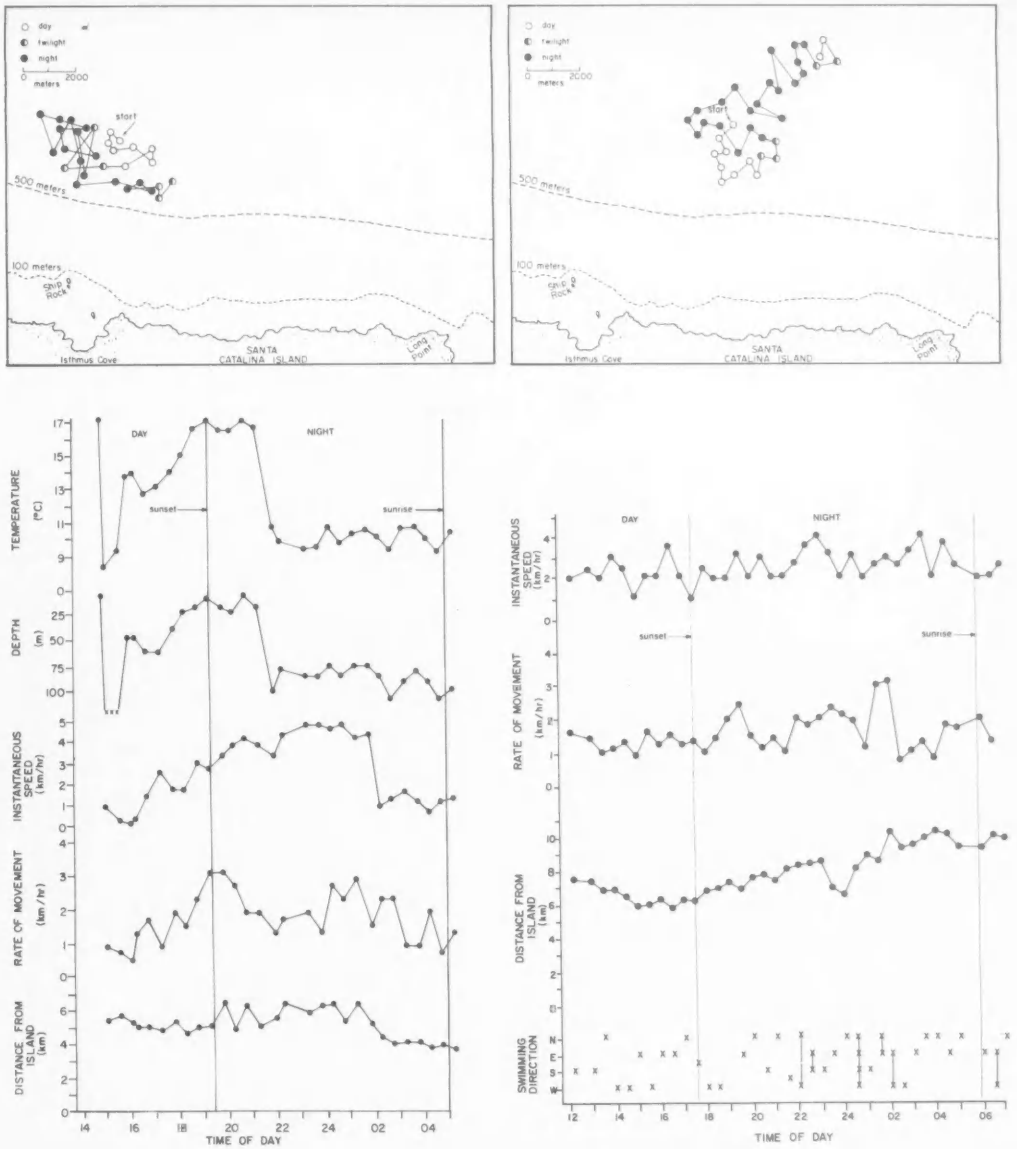

FIGURE 4.—Data from two individual trackings of blue sharks typical of the late June to early October period. Top, shark positions at approximately 0.5-h intervals. Bottom, telemetered sensor data. Note the absence of shoreward movement, the increased swimming speed and depth at night (left), and the greater frequency of sudden direction change, i.e., multiple-direction recordings, at night (right).

the day, e.g., on blacksmith, *Chromis punctipinnis* (R. R. Given pers. commun.; D. R. Nelson unpubl. data) and on northern anchovy, *Engraulis mordax* (T. C. Sciarrotta unpubl. data).

The large size of the blue shark's eye suggests adaptation to low light, as in general, nocturnal fishes have relatively large eyes. However, large eyes are also associated with moderately deep

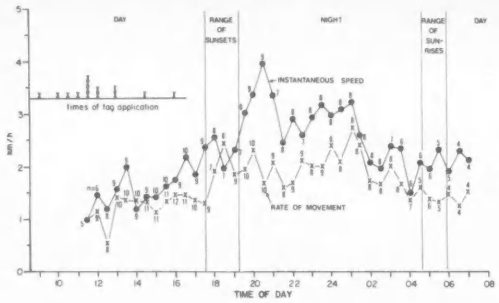

FIGURE 5.—Comparison of mean rate of movement (all sharks) and telemetered swimming speed (sharks with speed sensors) for blue sharks. Note the increase in both parameters at night, the greater values for swimming speeds (as expected), the close similarity during times corresponding to shoreward movements (relatively straight swimming), and the large disparity in early evening (relatively nonstraight swimming).

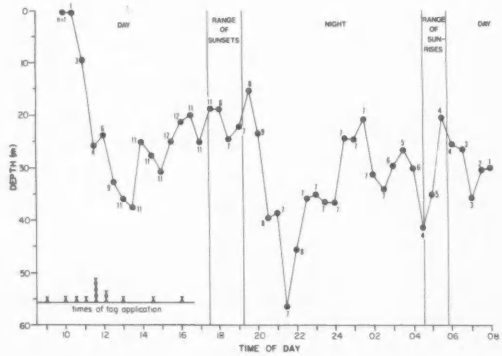

FIGURE 6.—Mean depths of all blue sharks tracked with transmitters having depth sensors. The first hour of each tracking is deleted because of the initial plunge in response to tag application. Note the generally greater depths at night.

habitat (mesopelagic), but since the blue shark's habitat appears relatively shallow (epipelagic), the large eye would seem best suited to visual hunting at night.

It is known that cephalopods and small pelagic fishes form a major part of the diet of blue sharks (Strasburg 1958; Stevens 1973; Tricas 1977). The observed seasonal differences in diel movement patterns (Figures 1, 3) may reflect differences in type or location of prey. Fishery landings of market squid, *Loligo opalescens*, were high during February to June 1972, but low from July to December (Pinkas 1974), thereby indicating the inshore presence of spawning congregations (Frey

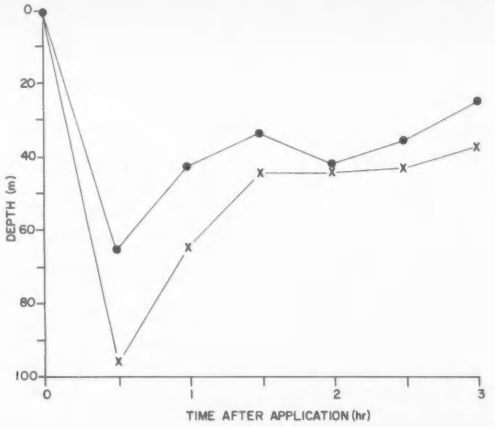

FIGURE 7.—Mean depths of blue sharks for the first 3 h of each tracking. Upper curve, all 12 sharks carrying transmitters with depth sensors. Lower curve, seven sharks judged to have made an "abnormal" plunge in response to the trauma of tag application. Note that the initial depth response appears to have subsided by the recording session 1.5 h after application.

1971), which are susceptible to commercial fishermen using night-lighting techniques. Cousteau and Cousteau (1970) described blue sharks gorging themselves on spawning squid that were light-attracted to the surface near their vessel.

The evening-twilight onshore movements which occurred during March to early June may be due to the nearshore abundance of squid and a possibly reduced availability of prey offshore. Conversely, the offshore pattern from late June to October may be a result of reduced squid population nearshore, but increased populations of jack mackerel, *Trachurus symmetricus*, and anchovy offshore. The limited stomach-content data collected during this study support this hypothesis.

In regard to depth/temperature preferences, the results of Strasburg (1958) are somewhat different from those of the present study. His longline catches of blue sharks at equivalent latitudes were from depths of 53 to 93 m (45%), 93 to 143 m (30%), and 123 to 166 m (25%). The blue sharks tracked in the present study appeared to exceed 93 m only about 5.1% of the time (excluding initial plunges). It is conceivable, however, that Strasburg's percentages may have been influenced by the sharks being attracted deeper than normal by the sloping odor corridors from baits on the gradually sinking longlines. That blue sharks on occasion go even deeper than Strasburg's deepest hooks was noted by Pethon (1970) who reported captures in Norwe-

gian waters from depths as great as 370 m. Davies and Bradley (1972) observed individuals at depths between 100 and 275 m during a descent in the submersible *Deepstar 4000*. A large school of northern anchovy was also observed in this depth range and a predator-prey relationship was suggested, although the possibility of the sharks following the descending submersible could not be eliminated.

In regard to temperature, Strasburg (1958) recorded 99% of his catches over the range of 7° to 20°C, with 67% between 10° and 15°C. Thus, temperature alone may not be reason for the apparent absence of blue sharks from the offshore study area during January and February 1972 when the surface temperature was about 13°C.

The navigational mechanism employed by the sharks during their island-oriented migration is unknown. Traditional explanations for such fish movements include sun-compass orientation, visual landmark recognition, and orientations to chemical or thermal gradients. None of these mechanisms seem plausible in view of the constancy of the pelagic environment, depths usually occupied during the movement, and the relative darkness in which the movements often occurred. Orientation to magnetic or electric fields is one possibility that must be considered in view of the recent findings of Kalmijn (1971, 1973) demonstrating magnetic/electric responses in sharks of adequate sensitivity for such a mechanism. Another possibility is orientation by passive acoustic means to the sounds of the island shoreline, in a manner similar to that suggested by Evans (1971) for dolphins.

The diel inshore-offshore migration shown by this study must also be considered in view of the much longer range movements exhibited by blue sharks. Individuals off California are known to segregate by sex, and seasonal changes in sex ratios imply seasonal north-south migration, perhaps in response to water temperature (Johnson 1974; Bane 1968; Tricas 1977). Tagged individuals have exhibited some very long-range movements. One blue shark tagged by Bane off Newport Beach, Calif. in July 1967 was recovered in December of the same year about 1,300 km west of Nicaragua. Another tagged by D. R. Nelson (unpubl. data) off San Diego, Calif. in October 1966 was recovered in October 1969 about 1,800 km west of the Galapagos Islands, a distance of 4,000 km from its tagging site. This shark was captured only 8 days short of a full 3 yr at liberty and, therefore, did not appear to be participating in any seasonal north-south migration. Both of the above sharks were recovered by Japanese fishing vessels, presumably longlining in relatively deep, cool water.

ACKNOWLEDGMENTS

We sincerely thank the many persons who contributed to this study, especially E. Standora (initial development and testing of telemetry system), H. Carter and D. Ferrel (circuit design), and J. Hall (assistance during trackings at sea). We also acknowledge the Office of Naval Research for financial support, through contract N00014-68-C-0318, under project NR-104-062, for the program of shark research of which this study is a part.

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A BIOENERGETIC MODEL FOR THE ANALYSIS OF FEEDING AND SURVIVAL POTENTIAL OF WINTER FLOUNDER, *PSEUDOPLEURONECTES AMERICANUS*, LARVAE DURING THE PERIOD FROM HATCHING TO METAMORPHOSIS

GEOFFREY C. LAURENCE[1]

ABSTRACT

A bioenergetic model was developed which simulated effects of temperature, prey density, and larval size on ability of winter flounder, *Pseudopleuronectes americanus*, larvae to obtain food energy to provide for experimentally determined growth and metabolism. Larval feeding at constant temperature and as a function of prey concentration was exponential and more sharply asymptotic in younger fish than in those near metamorphosis. Specific growth rates were exponentially related to prey concentrations and ranged from 5.72 to 8.70%/day at survival prey concentrations of 3.7 to 21.7 cal/liter. Daily required feeding time was directly related to prey availability. Critical plankton densities below which larvae did not have enough time during the day to obtain adequate food for growth and metabolism varied with age and ranged from 2.1 to 5.7 cal/liter. Simulated physiological energy utilization and required caloric food intake were inversely related to prey concentration and varied with larval stage of development. Food requirements expressed as numbers of copepod nauplii consumed per day ranged from 19 for first feeding larvae to 235 for metamorphosed juveniles. Predicted gross growth efficiencies were directly related to prey concentration and increased with age from 5 to 33%. All indications pointed to a "critical period" of larval survival during the period of exogenous feeding initiation and immediately after.

One of the important problems in fishery research and management is identifying and understanding the functional mechanisms of the stock–recruitment relationship. It is becoming more apparent that focusing attention on studies of mortality in the early life stages, particularly the larval stage, may help in this understanding. Mortality rates are usually the highest and most variable from year to year during the early life stages. Because of this, even small changes in mortality during this period can produce a magnified effect on the eventual numbers of recruits to sport or commercial fisheries.

Other than predation, the most important probable factors influencing larval mortality are food and feeding relationships and the influence of environmental parameters on these processes. The acquisition of the required food ration by fish larvae is of prime importance in survival and successful development. Without the proper quantity and quality of food, larvae will be adversely affected and survival will be influenced. Bioenergetic relationships have been studied extensively for adult fishes, and the works of Ivlev (1939a, b, c), Winburg (1956), Paloheimo and Dickie (1966a, b), and Warren and Davis (1967) are among the most complete. However, the use of energy resources in physiological mechanisms and the relationships of feeding, growth, and survival in the early life stages of fishes have only recently been studied (Ivlev 1961a, b; Lasker 1962; Laurence 1969, 1973).

It is the object of this research to examine the effects of food and feeding on winter flounder, *Pseudopleuronectes americanus*, survival from the period of hatching to metamorphosis and to develop a model of these critical processes. The model includes the forcing variables of temperature, prey density, and larval size or age and their effects on the ability of winter flounder larvae to successfully acquire energy rations necessary for experimentally determined growth and metabolic parameters. The energy rations are quantified as to caloric value of ration, numbers of specific prey organisms consumed, time for required intake, and metabolic parameters dealing with conversion into fish flesh.

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MATERIALS AND METHODS

Adult winter flounder were captured by trawl net from Narragansett Bay, R.I., and maintained in 1,900-liter experimental aquaria. Embryos were obtained by allowing the fish to ripen naturally under optimum temperature and photoperiod conditions or causing ovulation with hormones according to the techniques of Smigielski (1975). Embryos were incubated with methods developed at the Narragansett Laboratory (Smigielski and Arnold 1972).

All experiments and rearing were done at 8°C during these studies since this temperature is the approximate mean temperature for the entire period from hatching to metamorphosis for winter flounder in the Narragansett Bay area. Stock cultures of larvae were reared in series of black 64-liter experimental aquaria. The aquaria were placed in an environmental room or in water baths where the temperatures were maintained by program recorders controlling heating and cooling coils. All experimental aquaria were aerated with air stones and were semiclosed systems with a portion of the seawater being replenished every 1 or 2 days. Illumination was controlled by timers which provided a 12:12 day–night photoperiod corresponding to the mean photoperiod during the normal winter flounder spawning time.

Zooplankton fed during all experiments consisted mainly of the nauplii, copepodites, and adults of the copepods *Acartia clausi, Centropages hamatus,* and a few *Temora longicornis* and *Eurytemora affinis* collected from the Narragansett Bay area with 0.5-m plankton nets fitted with 64- and 116-μm mesh. Collections were sieved through 200- or 500-μm mesh strainers, depending on the size of larvae to be fed. Plankton densities in experimental aquaria were monitored by taking two to four 5-ml aliquots from the aquaria and counting the number of plankters under a dissecting microscope.

The relationship between larval size (body dry weight) and stomach contents was studied from hatching to metamorphosis. Larvae were reared in a 64-liter black aquarium and were fed high prey concentrations of 13.6–20.5 cal/liter or approximately 2 or 3 nauplii/ml. Samples of 25 larvae were taken each week until metamorphosis for stomach analyses and dry body weight determinations.

Experiments determining the influence of prey concentration on daily feeding intensity expressed as stomach contents were conducted at 0.68, 3.41, 6.80, 20.5, 34.1, and 47.8 cal/liter (corresponding to 0.1, 0.5, 1.0, 3.0, 5.0, and 7.0 nauplii/ml). Larvae aged 2, 5, and 7 wk after hatching were used. Approximately 25 larvae were placed in all black 4-liter aquaria containing the desired prey densities. The larvae were allowed to feed for 1 day's photoperiod (12 h) after which they were pipetted onto a 100-μm mesh screen and allowed to suffocate to prevent regurgitation of food before being preserved in 5% Formalin.[2] Ten larvae from each prey concentration were used for stomach analyses and 10 were used for mean dry body weight determinations. Stomach analyses were done with a dissecting microscope. Larval stomachs and intestines were teased apart with fine needles, and contents were identified to genus and species if possible.

Digestion rate measured by gut clearance time of larval winter flounder at 8°C was determined by feeding dyed zooplankton according to the techniques of Laurence (1971a). Transparency of the larvae permitted visual observation of dyed plankters in stomachs of living larvae. To determine the evacuation time of the stomach and intestine under active feeding conditions, larvae feeding on dyed plankters at concentrations of 1 or 2 nauplii/ml were removed and placed in duplicate aquaria with similar concentrations of nondyed plankton, and the gut clearance times of the dyed plankters from individual larvae were recorded.

Experiments determining the influence of temperature on growth of winter flounder larvae were conducted in 38-liter experimental aquaria. Feeding, monitoring, and sampling techniques and results for these experiments are described in detail by Laurence (1975).

The influence of planktonic prey concentration on growth and survival at 8°C from the period hatching to metamorphosis was studied at prey concentrations of 0.068, 0.68, 3.41, 6.80, and 20.5 cal/liter, corresponding approximately to 0.01, 0.1, 0.5, 1.0, and 3.0 nauplii/ml. Larvae were stocked at an initial density of 500 per aquarium; methods for maintaining prey concentrations, sampling, and determining growth and survival rates are described in detail by Laurence (1974).

Standard manometer equipment (Warburg res-

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

pirometers) and techniques (Umbreit et al. 1964) were used to measure oxygen consumption for metabolic determinations in relation to temperature and larval size. A description of the specific methods and results has been reported earlier (Laurence 1975).

All combustions for caloric determinations of larval winter flounder tissue were done in triplicate in a Parr 1241 automatic adiobatic calorimeter adapted for a microbomb. Caloric values for copepod prey species and methodology for these determinations are reported by Laurence (1976).

All statistical analyses used in this research are described in Steel and Torrie (1960) and Draper and Smith (1966). Modeling and analyses were done in the FORTRAN IV language on an IBM 370 computer.

EXPERIMENTAL RESULTS

Food Consumed and Relationship to Larval Size

Numerical analysis of stomach contents is not very meaningful in itself. It can, however, be useful in conjunction with the measurement of other parameters. An estimation of the dry weight and caloric value of food consumed per larval dry weight was needed as part of the overall bioenergetic model. Stomach analysis by enumerating copepods in larvae fed high concentrations (2 or 3 nauplii/ml) combined with information on dry weights and caloric values of the copepods provided this. Mean dry weights for the copepod species and life stage were taken from the literature (Conover 1960; Anraku 1964; Hargrave and Geen 1970; Gaudy 1974). Caloric values were determined in our laboratory (Laurence 1976). The average composite values used for the copepods in this study were 1.3 μg dry weight for nauplii, 15.4 μg dry weight for older stages, and 5,251 cal/g dry weight for all copepod tissue. Multiplying the numbers of plankton species and life stage per stomach by the average dry weight values for each plankter type and summing yielded the mean dry weight of the stomach contents. Results of these analyses along with nauplii to older stage ratios of copepods consumed and caloric value per stomach are shown in Table 1. The regression relationship of the logarithms of larval dry body weight and larval stomach contents weight was positively linear (Figure 1) and significantly correlated ($R = 0.87, P = 0.01$).

TABLE 1.—Mean numbers, weights, and caloric values of copepods consumed by larval winter flounder of different sizes. Each sample consists of 25 larvae.

Mean larval dry wt (μg)	Mean no. of copepods per stomach	Nauplius to older stage ratio	Mean dry wt per stomach (μg)	Calorie per stomach
10.4	2.0	1:0	2.6	0.0137
14.3	1.0	1:0	1.3	0.0068
21.5	2.1	1:0	2.7	0.0142
29.4	5.4	1:0	7.0	0.0368
51.1	3.3	29:1	6.0	0.0315
81.2	32.3	12:1	41.9	0.2205
226.8	2.9	12:1	6.9	0.0362
396.6	4.7	3:4	43.8	0.2300
444.2	33.5	22:1	57.7	0.3030
513.9	8.4	1:2	89.9	0.4720
667.6	3.0	1:2	32.1	0.1686

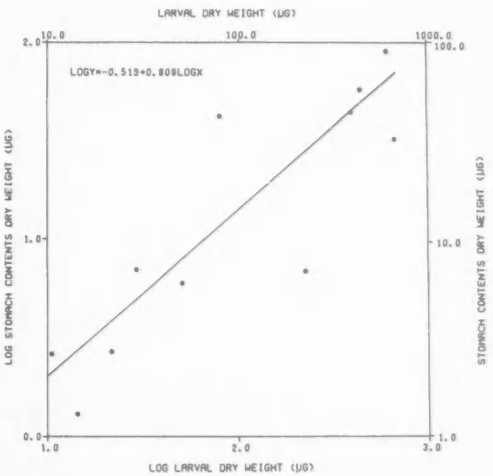

FIGURE 1.—The regression relationship of larval dry body weight to larval stomach contents weight for winter flounder at 8°C.

Prey Density and Intensity of Feeding

The relationship between intensity of feeding and concentration of prey is important in determining food intake. Ivlev (1961b) has analyzed this relationship and expressed it by the following function:

$$\frac{dr}{dp} = \alpha(R - r)$$

where r = size of a unit ration for a unit time
R = maximum size of the ration during the same unit time at the upper limiting level of food concentration beyond which ration size does not increase

α = coefficient of proportionality
p = plankton concentration.

After integration, the function becomes:

$$r = R\ (1 - e^{-\alpha p}).$$

Use of this relationship in analyzing winter flounder feeding as influenced by prey densities of 0.68–47.8 cal/liter, or 0.1–7.0 nauplii/ml, yielded some interesting results (Figure 2). Feeding was reasonably constant in the youngest fish with an asymptote being reached quickly at the lower prey concentrations. Five-week-old larvae displayed a rather classic form of the Ivlev curve with food intake increasing with prey density, reaching a maximum at approximately 6.8 cal/liter or 1.0 nauplius/ml, and then remaining quite stable. The oldest larvae, prior to metamorphosis, showed an increasing food intake through the whole range of plankton densities, right up to 47.8 cal/liter or 7.0 nauplii/ml. In general, there appeared to be an increasing of the upper limiting level of food concentration and a decreasing of the coefficient of proportionality (α) with increasing larval age.

Digestion Rate

Winter flounder larvae were known to be continuous, visual daylight feeders from prior research. Preliminary attempts at establishing digestion rates and unpublished results of night feeding experiments showed that larvae at-

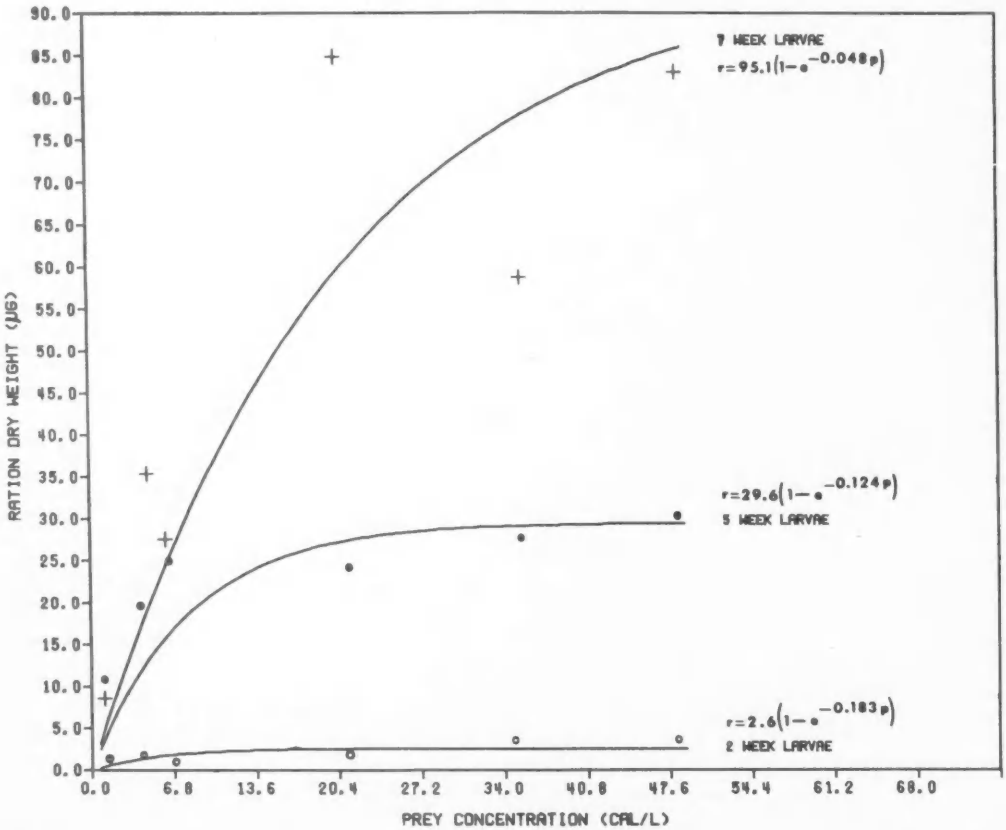

FIGURE 2.—The relationship between planktonic prey concentration and feeding intensity expressed as stomach ration for different aged winter flounder larvae at 8°C.

tempted to feed constantly under daylight conditions and ceased feeding entirely during darkness. Evacuation rates of the gut while larvae were actively feeding were recorded at 8°C for estimates of digestion rates. Results of 10 individual larvae showed a mean, active digestion time of 6.6 h with a range of 5.1–8.4 h.

Effects of Prey Density on Growth and Survival

The effects of five prey densities from 0.068 to 20.5 cal/liter (approximately 0.01–3.0 nauplii/ml) on growth and survival of winter flounder larvae from hatching to metamorphosis at 8°C were examined. Larval survival did not exceed 2 wk at the lower two densities of 0.01 and 0.1 nauplius/ml. Growth expressed as dry weight against time at the three survival densities (3.4, 6.8, and 20.5 cal/liter) was similar (Figure 3), as indicated by the confidence intervals about the slopes of the descriptive regression equations (Table 2). Specific growth rates on a daily basis increased with plankton concentration and were experimentally observed to be 8.62%/day for 3.0 nauplii/ml, 7.68%/day for 1.0 nauplius/ml, and 5.72%/day for 0.5 nauplius/ml.

Plankton density influenced survival more significantly than growth. Specific mortality coefficients calculated by the methods of Laurence (1974), which correct for the number of experimental removals for growth measurements, demonstrated a direct relationship with lower mortality rates at each higher plankton density (Table 3). Plots of predicted specific mortality coefficients through the range of plankton densities from 0.68 to 20.5 cal/liter based on the above results yielded an exponential relationship (Figure 4).

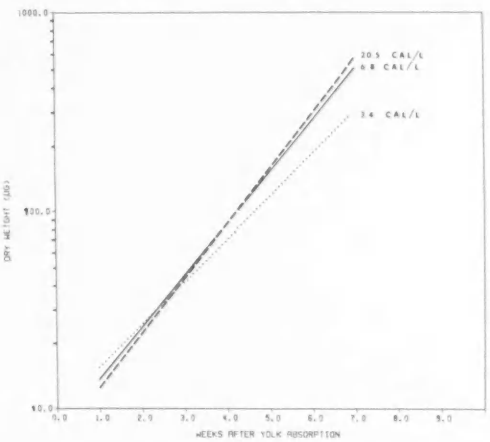

FIGURE 3.—Growth of winter flounder larvae at 8°C and at three different planktonic prey densities.

TABLE 2.—Regression equations and statistical parameters of winter flounder dry weight growth vs. time at 8°C and different planktonic prey densities.

Planktonic concentration (cal/liter)	Growth regression equation	Confidence interval about slope	Correlation coefficient
20.5	$\log Y = 0.849 + 0.269X$	0.212–0.326	0.98
6.80	$\log Y = 0.830 + 0.272X$	0.234–0.311	0.99
3.41	$\log Y = 0.990 + 0.208X$	0.141–0.275	0.97
0.68	No survival to metamorphosis		
0.068	No survival to metamorphosis		

TABLE 3.—Daily mortality coefficients of winter flounder at 8°C as influenced by planktonic prey density.

Planktonic concentration (cal/liter)	Corrected number of survivors out of 500	Days of survival[1]	Specific mortality coefficient
20.50	171	49	0.022
6.80	19	49	0.069
3.40	13	42	0.091
0.68	5	15	0.307

[1]No calculable survival at the lowest plankton density of 0.068 cal/liter.

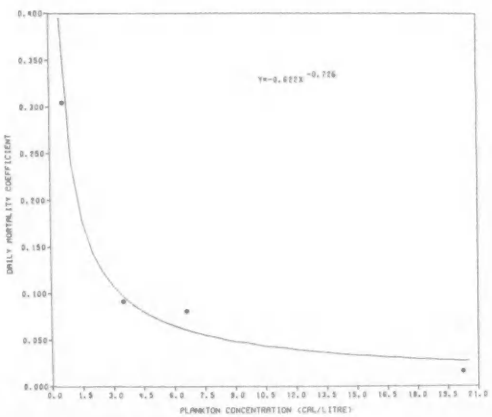

FIGURE 4.—Daily mortality coefficients of winter flounder at 8°C from the period hatching to metamorphosis as influenced by prey density.

Metabolic Rate

Laurence (1975) expressed metabolism of winter flounder from hatching through metamorphosis in terms of oxygen consumption. Regression relationships of mean hourly oxygen

consumption in microliters from hatching through and beyond metamorphosis on dry body weight were nonlinear and fitted best by a third-degree polynomial (Figure 5 from Laurence 1975). A third-degree polynomial was statistically most significant, as indicated by analysis of variance (F = 13.2 for cubic term, 7.4 for quadratic term, and 9.5 for linear term) over the weight range studied (10–4,000 μg). However, in this research the size range for larvae was 10–1,000 μg, and only the predicted data from the first ascending leg of the polynomial at 8°C were used in the computations.

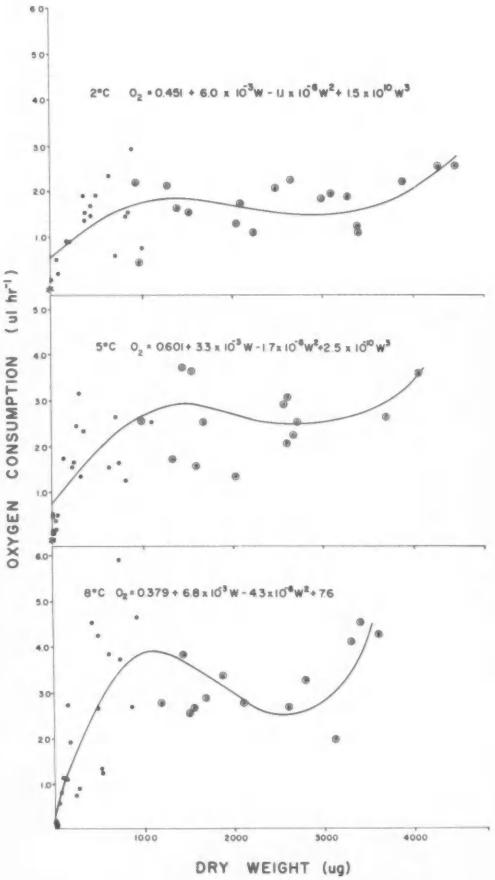

FIGURE 5.—Regression of mean hourly oxygen consumption on dry weight of winter flounder larvae and juveniles at three temperatures. Circled data points indicate metamorphosed juveniles. Results at 8°C used in these studies. (From Laurence 1975.)

BIOENERGETIC MODEL

A general model for the transformation of food to fish flesh and the energy relationships involved has been discussed in detail by Winburg (1956) and Warren and Davis (1967). The basic relationship can be expressed as:

$$Q_+ = Q_* + Q' + Q_- \quad (1)$$

where Q_+ = energy of food consumed
Q_* = energy of waste products in feces and urine
Q' = energy of growth
Q_- = energy of metabolism.

Since a portion of the energy value of food is lost in the feces and urine and not utilized or assimilated, Winburg (1956) proposed the following "balanced equation":

$$Q_+ - Q_* = Q' + Q_- \quad (2)$$

or

$$bQ_+ = Q' + Q_- \quad (3)$$

where b = the coefficient of utilization or, in Brody's (1945) terminology, the physiological useful ration. Equation (3) analyzes the conversion of food energy inside the fish (physiological). However, influences of the environment on food consumption and utilization must also be considered. Many modifications based on my experimental results and additions of methods of other researchers have been incorporated into a model suitable for a broader analysis of the bioenergetics of winter flounder larvae. The following paragraphs present a detailed description of the methods used to derive this model.

Ivlev (1961b) formulated a model founded on the basic bioenergetic equation (Equation (3)) for the utilization of food by plankton-eating fishes. The relationship is:

$$0.7Q_+ = Q' + Q_-. \quad (4)$$

The coefficient of utilization (b) is assumed to be 0.7, based on information provided by Ware (1975) who reviewed the most recent thinking of the efficiency of food conversion. During the course of a day, a larval fish will be active in daylight (while feeding) and relatively passive the remainder of the time (usually at night). It can be assumed that the intensity of metabolism dur-

ing rest is represented by the standard metabolic rate (Q_s) and active metabolism by the active rate (Q). Thus, if it is assumed that a fish actively feeds for a given number (a) of hours, the total daily expenditure of energy for metabolism can be defined as:

$$Q_{-} = a(Q - Q_s) + 24Q_s. \quad (5)$$

The basic Equation (4) can then be rewritten as:

$$0.7Q_{+} = Q' + a(Q - Q_s) + 24Q_s. \quad (6)$$

Also, the energy of food consumed (Q_{+}) can be equal to the sum of the hourly rations, r (see Prey Density and Intensity of Feeding), or $Q_{+} = ar$, and thus:

$$Q_{+} = aR(1 - e^{-\alpha P}). \quad (7)$$

Solving Equations (6) and (7) simultaneously by equating the Q:

$$\frac{Q' + a(Q - Q_s) + 24Q_s}{0.7} = aR(1 - e^{-\alpha P}) \quad (8)$$

is obtained. Thus:

$$a = \frac{Q' + 24Q_s}{0.7R(1 - e^{-\alpha P}) - (Q - Q_s)}. \quad (9)$$

Deriving the value of a, a number of different parameters can be computed. They are: 1) critical plankton density below which growth, metabolism and subsequent survival would be adversely affected, 2) food intake, 3) energy expenditure, 4) nonassimilated energy, 5) growth efficiency, 6) percent body weight eaten, and 7) the number of a given plankton species and life stages eaten per day. The following is a step by step explanation of the modifications used to compute these parameters at 8°C for larval dry weight from 10 to 1,000 μg (corresponding to the time period hatching to metamorphosis), for plankton concentrations from 0.5 to 21.7 cal/liter (approximately 0.1–3.0 nauplii/ml), and for growth, metabolic and digestion rates observed in laboratory experiments at 8°C.

1. Stomach contents weight in micrograms of planktonic prey eaten by a given size larva was computed from the regression equation presented in Figure 1.

2. The stomach contents weight per hour, or weight of food consumed per hour, was calculated from a modification of Bajkov's (1936) digestion equation. The modified equation is:

$$F = \frac{ST}{H} \quad (10)$$

where F = weight of food consumed per hour
S = average weight of food in the stomach at the time of sacrifice
T = feeding time in hours
H = number of hours necessary for food to be evacuated from the stomach at a given temperature = 6.6 h at 8°C for actively feeding winter flounder larvae.

Unpublished experiments indicated that winter flounder larvae fed only in daylight hours. Therefore, it was assumed that T was equal to 12.0 h in these experiments, or the approximate number of mean daylight hours in the period mid-February to mid-April, when winter flounder spawn. Also, F was considered to represent the maximum ration of a larva, or R (Prey Density and Intensity of Feeding section, Equations (7)–(9)).

3. R was converted to a caloric value by multiplying by 0.0052519 cal, or the average caloric value/microgram of the copepod species inhabiting Narragansett Bay and serving as potential prey for winter flounder (Laurence 1976).

4. The coefficient of proportionality (α) in Equation (9) was found to change linearly in a negative manner with increasing larval size (see Prey Density and Intensity of Feeding) and was correspondingly adjusted.

5. The growth increment, Q', was computed by multiplying the weight of a larva by the specific growth rate at 8°C for the specified plankton density (see Effects of Prey Density on Growth and Survival). This was converted to calories by multiplying by 0.0050026, or the caloric value for winter flounder tissue as determined in laboratory combustion experiments with a bomb calorimeter.

6. Metabolism for a larva of given weight was calculated from the regression equations for oxygen consumption and weight (Laurence 1975; Figure 5) and converted to calories by multiplying by 0.005 which represents the caloric equivalent of 1 μl of oxygen for the full range of respiratory quotients associated with the utilization of fats,

carbohydrates, and proteins (Swift and French 1954). Active metabolism (Q) was derived by multiplying standard metabolism (Q_s) measured in the oxygen consumption experiments by 2.5. Fry (1947) showed that the active metabolism in small fishes was about twice the standard rate. More recently, however, Ware (1975) demonstrated in a re-analysis of Ivlev's (1961b) data that active metabolism calculated for a variety of growth rates and feeding densities could vary between 2 and 3 times the standard rate. Recognizing that active metabolism is a dynamic factor, it is not unrealistic to assume a multiplier of 2.5 times standard metabolism for an estimate of active metabolism.

7. The number of hours (a) a larva of given weight needed to feed to attain a given growth rate at a given temperature and plankton concentration was computed from Equation (9).

8. Since winter flounder larvae were observed in experiments to be visual feeders, the plankton densities for each weight which predicted 12.0 h feeding time (a) were identified. These were considered critical densities because feeding times longer than this were ecologically impossible due to unsuitable photoperiod.

9. Food intake in calories was computed from Equation (7).

10. Metabolism or energy expenditure was computed from Equation (5).

11. Nonassimilated energy was computed by subtracting the energies of growth (Q') and metabolism (Q_-) from the energy of food intake (Q_+).

12. Gross growth efficiency was calculated from the formula:

$$K_1 = \frac{Q'}{Q_+}$$

where K_1 = gross growth efficiency and Q' and Q_+ are as previously defined.

13. The percent body weight eaten per day was calculated by dividing the caloric value of food intake (Q_+) by the caloric value of the given body weight.

14. The number of naupliar or adult copepods consumed per day at the given parameters was calculated by dividing the caloric value of the food intake (Q_+) by the previously defined average caloric value for nauplii or adults.

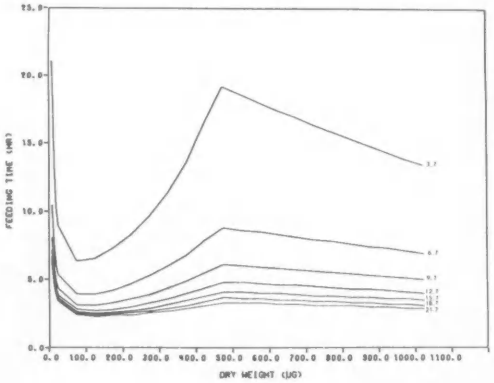

FIGURE 6.—Number of daily feeding hours required by winter flounder larvae to obtain energy for calculated growth and metabolism as influenced by larval dry weight and planktonic prey concentration at 8°C. Numbers for each simulated line indicate prey concentration in calories per liter.

MODEL SIMULATION RESULTS

Daily Feeding Time and Critical Prey Densities

The number of daily feeding hours required to meet growth and metabolism (a, Equation (9)) in relation to larval dry weight and at plankton densities which allowed feeding at some time within the limits of the 12-h day length simulated by the model is plotted in Figure 6. Feeding time at all plankton densities was initially high for the younger, smaller fish which later decreased before increasing again to a peak around 500 μg dry weight, or when metamorphosis starts to take place. A gradual decrease occurred during the metamorphosis period (500–1,000 μg larval dry weight). As was expected, required daily feeding times decreased with increasing prey density.

The critical, minimal prey densities below which longer than 12 h would have been required to obtain energy to meet growth and metabolism over the range of weights showed the highest critical densities during the period corresponding to first feeding with a decrease to a minimum shortly after (10–75 μg larval dry weight, Figure 7). An increase was then noted until the beginning of metamorphosis (500 μg) after which the critical prey density gradually decreased to complete metamorphosis (1,000 μg). The range of critical, minimum densities for the whole period was from 2.1 to 5.7 cal/liter, or approximately 0.3 to 0.8 nauplius/ml.

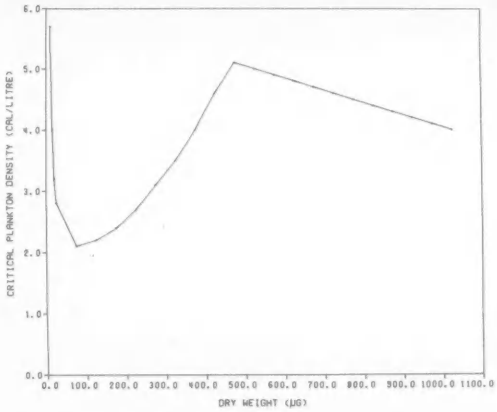

FIGURE 7.—Critical, minimum prey densities, below which feeding longer than the available photoperiod would permit to obtain energy for calculated growth and metabolic processes, over the weights range from hatching to metamorphosis for winter flounder at 8°C.

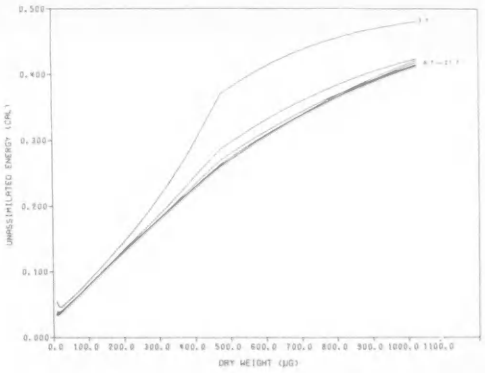

FIGURE 9.—Nonassimilated energy of winter flounder larvae at 8°C over the range of dry body weight from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 cal/liter simulations are in ascending order from top to bottom.

Physiological Energy Utilization

Predicted daily metabolic energy utilized by winter flounder larvae from hatching to metamorphosis ($Q_$, Equation (5)) showed a decrease shortly following hatching which later increased until initiation of metamorphosis when there was a leveling off (Figure 8). Energy expended was substantially higher at the lower prey concentrations with the differences minimized with increasing concentration. Predicted daily unassimilated energy, or energy not utilized in physiological processes and lost to the larval system, followed a similar trend to metabolic energy (Figure 9). In general, the ratio of nonassimilated to metabolic energy overall factor combinations was approximately 1:2.

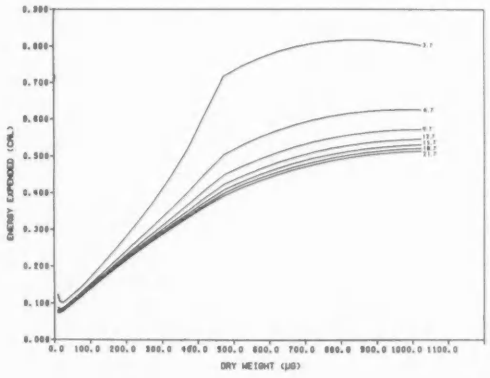

FIGURE 8.—Metabolic energy utilized by winter flounder larvae at 8°C over the range of dry body weight from hatching to metamorphosis and at different plankton concentrations. Numbers for each simulated line indicate prey concentration in calories per liter.

Required Food Ration and Growth Efficiency

Predicted daily caloric food requirements (Figure 10, Equation (7)) after an initial decrease following first feeding (10–30 μg dry weight) increased until the beginning of metamorphosis (500 μg), after which the rate of increase slowed until complete metamorphosis (1,000 μg). Food requirements were greater at lower prey concentrations with decreasing differences at higher concentrations. Conversion of caloric values of daily food requirements by division by mean caloric values of the copepod life stages per unit weight showed the numbers of nauplii or older stages necessary for consumption (Figure 11). Actual feeding experiments demonstrated that larvae do not prey entirely on one particular copepod life stage. The stages they consume are more a function of larval and copepod size. Smaller larvae initiate feeding on nauplii and gradually eat increasingly greater percentages of

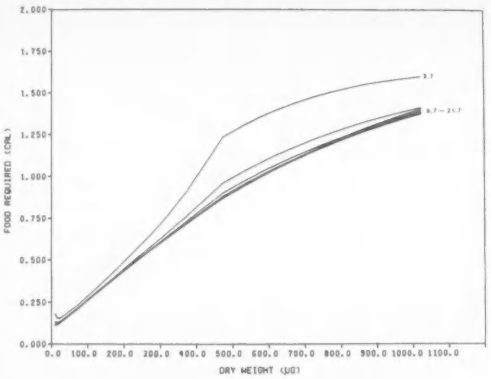

FIGURE 10.—Daily food requirements of winter flounder larvae at 8°C over the range of dry weight from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

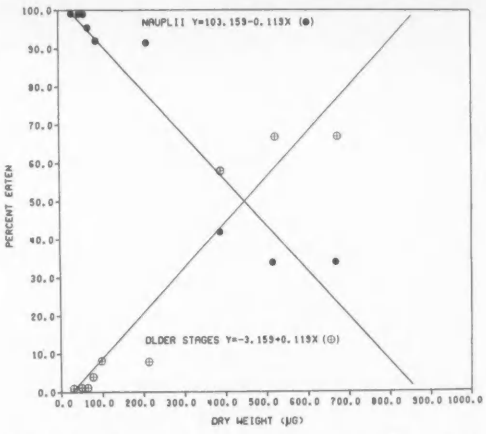

FIGURE 12.—Regression relationships of percentages of nauplii and older stage copepods eaten by winter flounder larvae of different sizes at 8°C.

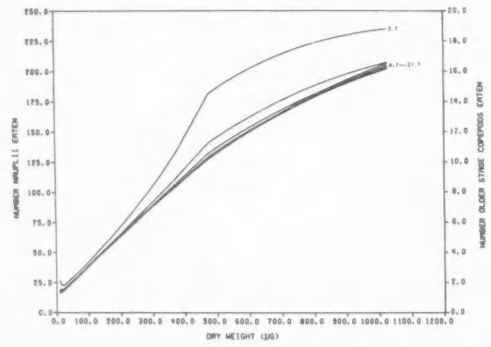

FIGURE 11.—Predicted number of nauplii or older stage copepods required for daily consumption by winter flounder larvae at 8°C over the range of dry body weights from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

older stage copepods as larval size increases (Figure 12).

The percentage of body weight consumed per day index (Figure 13) demonstrated sharply decreasing values during the first weeks of life (10–75 μg), after which values remained fairly stable until metamorphosis. More food was consumed per body weight at lower plankton densities. The differences became minimal with increasing plankton density.

Predicted gross growth efficiencies increased sharply from first feeding until a dry body weight of 100 μg, after which they continued to increase but at a decelerated rate (Figure 14). Efficiencies were lower at lower plankton concentrations, and the differences became smaller as plankton concentration increased.

DISCUSSION

A majority of the prior research has dealt with instantaneous estimates of larval food needs (Chiba 1961; Braum 1967) rather than a descriptive relationship over the range of larval sizes from hatching to metamorphosis. Larval winter flounder exhibited a linear increase in food consumption, as indicated by stomach contents with increasing size (Figure 1). A linear relationship was also reported for larval largemouth bass, *Micropterus salmoides* (Laurence 1971b). Stepien (1974) observed an exponential increase for the larvae of sea bream, *Archosargus rhombodalis*, at much higher temperatures (23°–29°C) than the 8°C studied for winter flounder in this research.

The amount of food a larval fish consumes during a day depends on the size of the fish and density of the prey organisms available (Ivlev 1961a, b). This is especially evident for winter flounder larvae for which the traditional Ivlev relationship changes with age or size (see Prey Density and Intensity of Feeding, Figure 2). Smaller, younger larvae reached maximum ration (R, Equation (7))

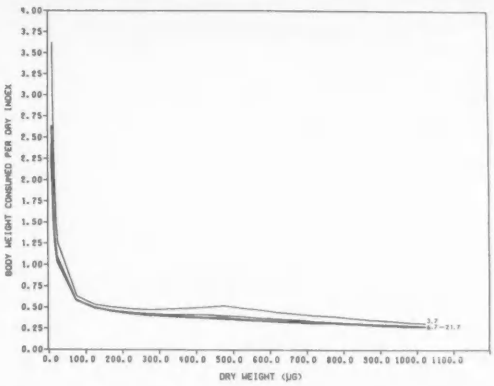

FIGURE 13.—Index of body weight consumed per day by winter flounder larvae at 8°C over the range of dry weights from hatching to metamorphosis and at different planktonic prey concentrations. Numbers for each simulation indicate prey concentration in calories per liter; 6.7–21.7 simulations are in ascending order from top to bottom.

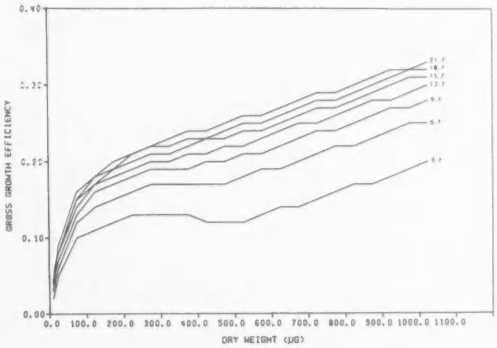

FIGURE 14.—Gross growth efficiencies of winter flounder larvae at 8°C over the dry body weights from hatching to metamorphosis and at different plankton concentrations. Numbers for each simulation indicate prey concentration in calories per liter.

at lower prey densities, while larger, older larvae approached maximum feeding ration at increasingly higher densities. The higher coefficient of proportionality (α, Equation (7)) values for the smaller larvae suggests that they have an easier time capturing their maximum ration. In fact, they reach their maximum ration at lower prey densities because their stomach capacity is very small and limited, while large larvae with greater stomach volumes can take advantage of higher plankton densities. From the standpoint of successful captures to obtain the maximum ration, smaller, younger larvae are actually much less efficient than larger.

This size effect on feeding ration over a range of prey densities has not been specifically examined for fish larvae before. Powers (1974) theoretically evaluated tha Ivlev relationship with laboratory feeding data for an amphipod, *Anisogammarus confervicolus*. He examined changing coefficients of proportionality (α) at constant maximum ration. The results showed that the asymptote is approached more quickly at higher α's, similar to the results noted in this research. Powers did not analyze maximum feeding ration as a function of animal size at changing α's. He did, however, state that animal size would probably have an effect since larger animals are better predators than smaller ones.

The initial sharp reduction in feeding times predicted by the model following hatching until a dry weight of 75 μg (Figure 6) was undoubtedly due to the increased ability of growing winter flounder larvae to capture prey. This is supported by Schumann (1965), who reported that larvae of Pacific sardine, *Sardinops sagax*, which were initially successful at feeding increased their searching ability and the probability of capturing a subsequent prey. The increase in predicted feeding times from 75- to 500-μg size was due to the exponential increase in metabolic rate for premetamorphosed larvae (Laurence 1975). The reduction in predicted feeding time from the initiation of metamorphosis until its completion (500–1,000 μg) was related to the decrease in absolute metabolism due to behavioral changes of metamorphosing winter flounder (Laurence 1975) and their greatly increased efficiency at capturing prey, which required less energy expenditure. The decrease in predicted feeding time with increase in prey concentration was due to the increased chance of prey encounter and capture. Zaika and Ostrovskaya (1972) also confirmed this for Baltic smelt and Pacific herring, *Clupea harengus pallasi*, larvae when they theoretically showed that the time spent searching for food decreased exponentially with an increase in food concentration.

Most larval fish have been reported as visual feeders (Houde 1973) and require daytime light intensities for optimum feeding (Blaxter 1969). In view of this, it is surprising that little research has been done on the relationship of feeding parameters and available time for feeding. Ivlev (1961b) combining field and laboratory data for

Atlantic herring, *C. harengus*, from the Gulf of Finland reported that, at observed plankton concentrations in the field, the calculated time of feeding was 15 h. This coincided exactly with the length of day. Laurence (1971a), working with the stipulation of a 14-h feeding period for largemouth bass larvae, found that prey concentrations of 7.0 cal/liter (400 organisms/liter) were limiting. The results of this research show that simulated critical prey densities, below which winter flounder larvae do not have enough daylight hours for feeding to meet growth and metabolic energy requirements, actually vary with age and stage of development (Figure 7). The critical densities range from a high of 5.7 (0.8 nauplius/ml) to a low of 2.1 cal/liter (0.3 nauplius/ml) when feeding behavior has been established but before growth and metabolic demands are high. Critical density then increases until initiation of metamorphosis when it remains fairly constant around 4.5 cal/liter (0.6 nauplius/ml). Results such as these have not been quantitatively reported in the literature before. Most previous laboratory studies for a variety of species delineate constant critical prey densities for the larval period usually in the range 0.1–1.0 organism/ml (Kramer and Zweifel 1970; O'Connell and Raymond 1970; Saksena and Houde 1972; Laurence 1974; Houde 1975), although Rosenthal and Hempel (1970) reported that prey densities for optimum feeding (not critical densities) for larval Atlantic herring were higher for younger than older larvae.

The critical prey densities for larval survival of approximately 0.5 organism/ml noted in this and the other cited laboratory research are somewhat disparate with densities described from field data. Lisivnenko (1961) noted that larval Baltic herring were much less abundant in years when prey abundance was <0.01 organism/ml. Sysoeva and Degtereva (1965) reported that the minimum abundance of *Calanus finmarchicus*, when the intensity of feeding of cod, *Gadus morhua*, larvae decreased, was from 0.01 to 0.005/ml and that a concentration of 0.02/ml provided sufficient food for survival. It is my opinion that the results reported for laboratory studies may be more accurate than the field study data presented thus far. The laboratory studies represent highly controlled experiments with accurate counts of prey organisms. On the other hand, the field studies give estimates of prey abundance which represent average densities over linear or oblique sampling distances. Planktonic prey organisms have contagious distributions and larvae may well be associated with "patches" of prey that are more densely concentrated than indicated by plankton net tows (Wyatt 1973). Many larval fish researchers feel that density dependent mechanisms control larval survival (Cushing and Harris 1973), and the concept of contagious distributions in which larvae and prey are associated in "clumps" that may or may not be associated and occupying the same area is one of the most logical ways to explain the fluctuations noted for natural larval mortality. Also, field zooplankton sampling designs rarely use nets with mesh smaller than 200 μm. Most of the significant food organisms utilized by larval fishes especially in the early stages are <200 μm in smallest dimension (Houde 1973) and would be lost in field sample estimates. Use of the plankton pump may prove to be more accurate in locating patches of zooplankton and sampling the size organisms that larval fish consume. Recently, Heinle and Flemmer (1975), using a moving plankton pump, reported concentrations of nauplii of *Eurytemora affinis* in the Chesapeake Bay area as high as 2.8/ml with concentrations of 1.0–1.8/ml not at all uncommon. These concentrations are more than adequate for good growth and survival of winter flounder larvae and many other larval species.

The initial, predicted decrease in metabolic energy expended (Figure 8) during the period of feeding initiation and shortly after (10–30 μg dry weight) is undoubtedly explained by the increased feeding success with experience by first feeding larvae. First feeding individuals have a lower success ratio of captures and have to expend more energy in searching for prey than older and more accomplished feeders. This success or fail period is critical to eventual survival and is relatively short in duration for winter flounder, occurring during the first 8 days after feeding begins at 8°C. The increase in metabolic energy expended from 30- to 500-μg dry weight after successful feeding establishment is due to normal increases in energy demand for all processes with rapid increases in size usually seen in larval fishes. The leveling off of metabolic energy demand during the metamorphosis period (500–1,000 μg dry weight) may be unique to flatfishes due to marked morphological and behavioral changes (Laurence 1975) and increased predatory efficiency requiring less energy expenditure.

The decrease in metabolic energy expenditure with increasing prey concentration is logically

explained by the increased chance of successful feeding at higher plankton concentrations and concurrent decrease in energy expended to obtain prey. Warren and Davis (1967) concurred with this type relationship, stating that the density of food determines an animal's energy cost in obtaining the food. Decreasing metabolism with increasing food concentration is contrary to reported laboratory studies using fish older than the larval stages. Paloheimo and Dickie (1966a) and Beamish and Dickie (1967), examining data from other researchers, concluded that higher average metabolic rates result at higher feeding rates. However, it may be presumptuous to assume this type relationship for fish larvae. Most older, nonplanktivorous feeding fishes, such as those referred to in the above citations, are satiation or periodic feeders. In fact, most of the experimental data cited above were for restricted daily diets at different levels. Larval fish, like the winter flounder, are active continuous feeders and the assumption in this model was continuous feeding at maintained prey densities. Older fish have more body reserves and can exist on maintenance rations to which they can adjust metabolically in contrast to larval fish which must feed continuously and are committed to growth or else die. In fact, the concept of maintenance probably is not relevant to larval fish feeding and energetics. So, it seems logical that fish larvae feeding continuously and committed to relatively high growth rates would optimize growth by reduced metabolic expenditure which would result from the increased contact and efficiency of capture at higher prey densities and resultant feeding levels. The research of Wyatt (1972) with plaice larvae tends to further support this concept. He noted that activity, which he attributed to food searching, decreased with increasing prey concentration.

The trends of nonassimilated energy over the range of weights and plankton concentrations in this research are similar to those for metabolic energy expenditure and food consumption (Figure 9). This is not surprising due to the interrelationships of these factors. The decrease in nonassimilated energy with increasing weight (10–30 μg) for first feeding larvae is apparently due to their initial inefficient digestion which improves with morphological development. Visual examination of food in the anterior portions of the digestive tracts of young larvae during the digestion rate studies indicated relatively intact nauplii. This has been observed for other larval fish species. Rosenthal and Hempel (1970) noted that the efficiency of digestion in Atlantic herring fed *Artemia* nauplii was very low compared with older larvae. Morphological development of the alimentary tract during the larval stage was studied by Nishikawa (1975) who noted an increase in stomach size and extension of the digestive tract as a whole in relation to increasing standard length. He postulated that these morphological developments cause a rapid increase in the function of the organs during the larval period. The subsequent increase in nonassimilated energy with size of winter flounder larvae is merely proportional to the increased ration.

Daily food requirements of winter flounder larvae were initially higher for the period associated with first feeding (10–30 μg, first 2–3 wk after hatching, Figure 10). These short-term higher requirements were due to the inefficient manner in which newly feeding larvae captured prey and the associated, higher energy expenditure. Researchers have reported that young fish larvae are much less adept and successful at capturing prey than older larvae. Braum (1967) showed that freshwater whitefish larvae, *Coregonus wartmanni,* increased their successful captures from 3 to 21% during the first 16 days of feeding. Schumann (1965) noted an obvious increase in proficiency at capturing food with increased age of Pacific sardine larvae. The reasons for increased success with age are increased visual perception of food organisms and increased locomotor abilities with advancing development (Blaxter 1965; Rosenthal and Hempel 1970). The subsequent increase in required ration with larval size was the result of normal increased energy demand of growth and metabolism associated with larger sized larvae. An interesting fact is the decrease in rate of food requirement noted in metamorphosing larvae (500–1,000 μg). This may be associated with the previously mentioned decrease in routine metabolic rate peculiar to flatfish larvae and increased efficiency of prey capture during the metamorphosis period. Riley's (1966) results for another flatfish, the plaice, *Pleuronectes platessa,* substantiate this observation. He noted declining ingestion rates and rations during metamorphosis.

Conversion of the caloric values of daily food required into numbers of nauplii or older stages consumed (Figure 11) showed, of course, the same trends for food required. This conversion does,

however, give a different perspective in that it shows the actual numbers of organisms that winter flounder larvae require on a daily basis. The differences in numbers between nauplii and older stages reflect the differences in sizes providing equivalent caloric intake. Also, winter flounder larvae did not feed entirely on nauplii, but changed in part to larger stage copepods as they grew older. Size selection of prey by larval fishes has been shown to be a factor of mouth size which increases with increased larval size (Shelbourne 1965; Blaxter 1969; Detwyler and Houde 1970; Shirota 1970). The numbers of nauplii consumed per day ranged from 19 to 235 over the range of sizes and plankton densities. These values are similar to requirements for other larval species (Chiba 1961; Braum 1967; Rosenthal and Hempel 1970), although temperature, larval species and size, and food organisms can account for variable results.

Decrease in percent food eaten per day with body weight (Figure 13) is in accordance with results of other researchers and was due to the relative decrease in the rate of food intake compared with the growth rate with larval development. Pandian (1967) observed decreases in percent eaten per day with increases in body size of *Megalops cyprinoides* and *Ophiocephalus striatus,* as did Laurence (1971b) for larval largemouth bass and Stepien (1974) for larval sea bream.

The percentages of body weight consumed per day predicted in this research were high from over 300% at the smallest larval sizes and lowest prey concentration to 27–31% at the higher prey concentrations and largest larval sizes. Percent body weight eaten per day is typically much greater for larval and juvenile fishes as compared with adults since there is a much higher energy demand for growth purposes (Winburg 1956). Stepien (1974), in the only other known comparable research on marine larvae, also reported high percentages. His results for sea bream at 29°C were from 222.4% for 2-day hatched larvae to 79% for 7-day-old larvae. Sorokin and Panov (1965) reported 40–60% body weight eaten per day by larval freshwater bream.

The gross growth efficiencies recorded in this research increased rapidly with size for the smallest larvae (10–75 μg) and then increased at a decelerated rate for the remainder of the larval period to metamorphosis (Figure 14). Increased gross growth efficiency at greater body weights observed in my experiments is contrary to the results of research with older fishes. Parker and Larkin (1959) stated that within any growth stanza the gross efficiency must decline with increasing size, as a greater portion of the food must be used in maintenance. This may not be true for larval fishes, as their development is so rapid that a large portion of the energy derived from food intake is used in growth. It is my opinion that larval fishes could not exist on a maintenance ration. Rapid growth is a definite prerequisite for successful survival in the environment of larval fishes, and they must either consume food at high levels with resultant rapid growth or die. The ability of larvae to increase their feeding efficiency with increased size could also contribute to greater growth efficiency.

Divergent opinions have been expressed by researchers concerning the relationship between growth efficiency and feeding level or prey concentration. Paloheimo and Dickie (1966b) stated that growth efficiency declined with increasing ration. Warren and Davis (1967) showed that growth efficiency increased to two-thirds the maximum feeding level and then decreased. Finally, Davies (1964) demonstrated that efficiency of digestion and absorption of food by goldfish, *Carassius auratus,* was improved by increasing food input over a given weight range. He postulated that secretion of digestive fluids was stimulated by the effects of increased food. In all cases the studies and analyses were done with adult fishes. Winter flounder larvae increased their gross growth efficiencies with increased plankton density similar to Davies' results. However, the causative mechanism was most likely the increased efficiency of prey capture with increased prey encounter at higher densities with resultant metabolic savings for growth rather than increased secretion of digestive fluids. Growth efficiency is most likely a dynamic factor not subject to generalizations and dependent on life stage, type of feeding strategy, or prey type.

The range of values of growth efficiency for larval winter flounder on this research were from 5 to 33%, depending on larval size and plankton concentration. These values are similar to those for other young fishes (Ivlev 1939a; Sorokin and Panov 1965; Edwards et al. 1969; Laurence 1971a; Frame 1973; Stepien 1974).

The above discussions have revealed that there are interrelationships between the bioenergetic parameters simulated by the model and that the whole system works in a circular pathway to

maintain an energy balance in the larva's body. Energy expended at a given temperature promotes growth and results in a metabolism that produces activity, which in turn acts on the planktonic prey to provide an assimilated food intake that supplies energy for metabolism and growth. The whole process at a given temperature is in turn influenced by the size or age of larvae and the planktonic prey concentration. A good example which depicts the effect of larval age or size on these interrelationships and one which points to a definite "critical period" shortly after hatching around the period of feeding initiation is shown in Figure 15. In this figure the caloric expenditures for the important bioenergetic parameters over the range of weights from 10 to 50 μg are summed for all plankton concentrations. A definite divergence of energy away from growth to metabolism and nonassimilation with a resultant increased food requirement is shown during early life (10–30 μg). This period coincides with first feeding and is the time when larvae need to grow at a fast rate because of their small size, fragility, and vulnerability to predators. This identified "critical period" is caused by a number of factors and interrelationships including: 1) developmental factors of which reduced visual perception and locomotor (swimming) abilities in young larvae prevent efficient prey capture compared with older and better developed larvae; 2) less efficient conversion of food to flesh because of higher metabolic expenditure associated with more searching due to less efficient prey capture; 3) less efficient digestion in young larvae causing a smaller fraction of the food to be assimilated and be available for potential growth. As the larvae grow larger and older, especially during the metamorphosis period (50–1,000 μg), they become more efficient at converting food to growth. The slopes of the lines connecting the simulated values of the important bioenergetic components summed for all prey concentrations over the weight range of hatching to metamorphosis in Figure 16 show that the rate of growth accelerates more rapidly towards food consumption rate than metabolic and nonassimilation rates with increasing larval size after the critical period.

In addition to the critical period, plankton density is an important determinant of larval survival and, of course, interacts crucially during the critical period. The overall influence of prey density is shown in Figure 17 where the caloric expenditures of the important bioenergetic parameters simulated by the model are summed over all weights at each plankton concentration. It can easily be seen that low prey densities strongly affect the dispensation of energy available from food consumption in comparison with high densities. A greater portion of the energy intake is utilized for metabolism and is not assimilated

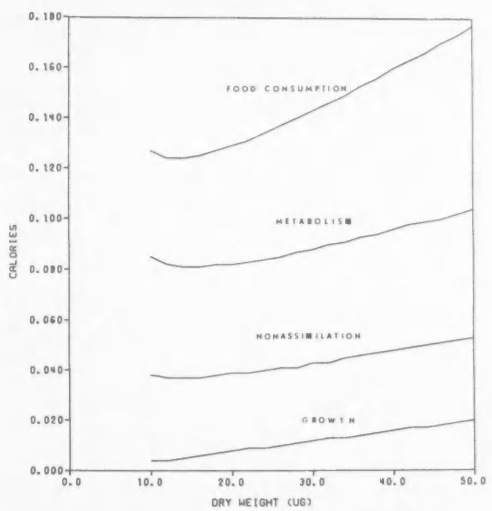

FIGURE 15.—Caloric energy expenditure for the major bioenergetic parameters of winter flounder larvae summed for all prey concentrations over the range of dry weights from 10 to 50 μg at 8°C.

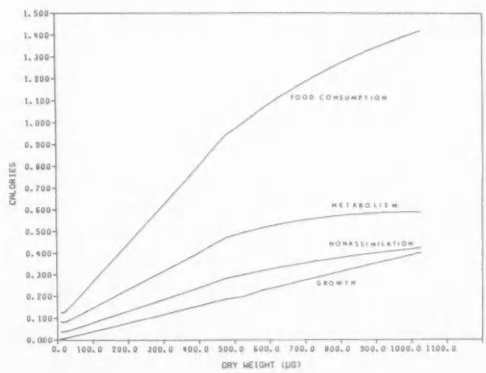

FIGURE 16.—Caloric energy expenditure for the major bioenergetic parameters of winter flounder larvae summed for all prey concentrations over the range of dry weights from hatching to metamorphosis at 8°C.

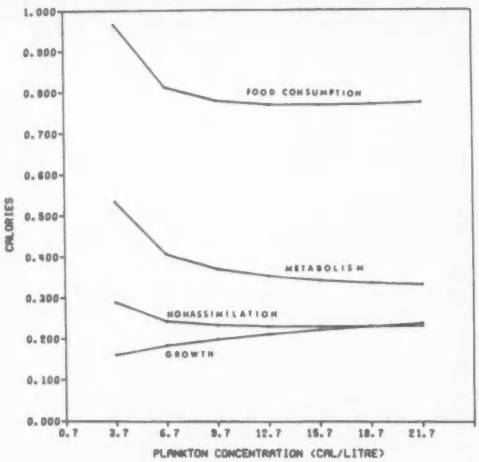

FIGURE 17.—Caloric energy expenditure for the major bioenergetic parameters at 8°C of winter flounder larvae summed for all dry weights from hatching to metamorphosis at different planktonic prey concentrations.

than is used for growth at lower prey densities. Also, the food requirements are higher at the lower densities which causes problems because food is harder to obtain at lower densities.

In conclusion, these experimental studies and model simulations demonstrate that there is strong evidence for a "critical period" of mortality in the larval stage of winter flounder and that planktonic prey density is one of the most important factors affecting survival during the larval stage. Additionally, the bioenergetic model developed presents a means to assess other trophic interactions in the marine, planktonic community. Larval fish are planktonic carnivores and the food requirements predicted by the model in combination with biomass estimates of larvae and prey and survival estimates of larvae can be used to predict the impact of larval grazing on their prey. This type of research is currently being pursued in continuing studies.

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DESCRIPTION OF LARVAL AND EARLY JUVENILE VERMILION SNAPPER, *RHOMBOPLITES AURORUBENS*[1]

WAYNE A. LAROCHE[2]

ABSTRACT

Larval and early juvenile development of vermilion snapper, *Rhomboplites aurorubens*, family Lutjanidae, is described and illustrated. Identification and description are based upon morphology, pigmentation, and meristics of 27 larval and 11 early juvenile specimens ranging from 4.0 to 14.2 mm standard length. All specimens were collected 65 km east of Sapelo Island, Ga., lat. 31°30′N, long. 80°30′W on 10 August 1972.

Larval and early juvenile vermilion snapper, *Rhomboplites aurorubens* (Cuvier), family Lutjanidae, are described from 27 larval and 11 small juvenile specimens collected at a station located approximately 65 km east of Sapelo Island, Ga., lat. 31°30′N, long. 80°30′W on 10 August 1972 (depth 22 m, surface temperature 26.7°C).

The genus *Rhomboplites* is monotypic and occurs only in the western Atlantic, from North Carolina and Bermuda to Rio de Janeiro, Brazil, including the Gulf of Mexico (Jordan and Evermann 1898; Hildebrand and Schroeder 1928; Hildebrand 1941; Anderson 1967; Böhlke and Chaplin 1968). Walker (1950) and Munro et al. (1973) reported *R. aurorubens* with mature ovaries during the cooler months, but Munro et al. (1973) suggested that some lutjanids may spawn throughout the year. I was unable to find any descriptions of lutjanid larvae. Small juveniles of the genera *Lutjanus* (Starck 1971; Heemstra 1974; Fahay 1975) and *Symphysanodon* (Fourmanoir 1973) have been illustrated.

METHODS

All specimens were collected by personnel aboard the U.S. National Marine Fisheries Service RV *Delaware II*. Ichthyoplankton was collected with a 60-cm diameter, 0.505-mm mesh, bongo net towed obliquely at 1.1 km/h (0.6 knot) from 20 m to the surface.

The specimens were stored in 3–5% buffered Formalin[3] after being removed from the sample (fixed in 10% buffered Formalin). Specimens were lightly stained with alizarin to facilitate measuring and counting body parts. One specimen (10.8 mm) was cleared and stained using the technique of Taylor (1967).

Illustrations were prepared using a camera lucida. Measurements were taken on the left side with an ocular micrometer. Measurements include:

Standard length (SL)—distance from tip of snout to posterior tip of notochord (before hypural formation) and tip of snout to posterior margin of hypurals (after hypural formation posterior to notochord tip).

Head length—distance (horizontal) from tip of snout to cleithrum.

Snout to anus—distance from tip of snout to posterior margin of anal opening.

Body depth—vertical distance between dorsal and ventral surfaces, to the ventral tip of the cleithrum.

Eye diameter—maximum diameter of eye.

Spine and fin ray lengths—distance from point of entry of spine or ray into flesh to distal tip.

IDENTIFICATION

Identification of the series was based on counts of small juvenile specimens which had 24 myomeres; 7 branchiostegal rays; XII, 11 dorsal fin

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spines and rays; III, 8 anal fin spines and rays; 17–18 pectoral fin rays; I, 5 pelvic fin spine and rays; 9+8 principal caudal fin rays. Taxa listed by Bailey et al. (1970) were checked for the counts listed above. Only *R. aurorubens* was found to have the above counts (Jordan and Evermann 1898; Hildebrand and Schroeder 1928; Anderson 1967; Böhlke and Chaplin 1968; Miller and Jorgenson 1973) among fishes inhabiting western North Atlantic waters less than 200 m deep. Larvae were linked to the juvenile specimens by similarities of morphology and pigmentation.

Future identifications of small larvae based upon this paper should be made with care since larvae of other lutjanids have not been described.

DESCRIPTION OF LARVAE AND JUVENILES

Only large larval and small juvenile stages are described since egg, yolk-sac, and small post yolk-sac stages were not available. Larvae are defined as all forms between yolk-sac absorption and differentiation of the adult complements of spines and soft rays in the fins. Transformation from larva to juvenile is gradually completed between 8.3 and 10.9 mm.

Pigmentation

Head pigmentation increases through the larval period (Figures 1, 2) with the smallest larva (4.0 mm) showing least pigmentation (Figure 1A). Head pigmentation includes a large stellate melanophore centered over the posterior portion of the midbrain and another on the ventral surface anterior to the tips of the cleithra (Figures 1, 2). The large dorsal melanophore is present on all larval and juvenile specimens except one which has a melanophore over each hemisphere of the midbrain on either side of the point where the central melanophore would be expected. A small area of internal pigmentation is also present ventral to the juncture of the midbrain and hindbrain. As the larvae increase in size, smaller stellate melanophores develop on each hemisphere of the midbrain anterior to the large central melanophore.

By 4.8 mm, a melanophore appears posterior to the dorsal tip of the opercle and 2 or 3 melanophores appear on the body beneath the opercle anterior to the cleithrum. Additional melanophores are added to the area of internal pigmentation ventral to the juncture of midbrain and hindbrain (Figure 1B).

There is a gradual increase of pigmentation over the forebrain and midbrain until melanophores form a cap of pigment over those structures (Figure 2B, C). From 15 to 20 melanophores per forebrain hemisphere and from 60 to 80 melanophores per midbrain hemisphere make up the cap in larger juvenile specimens (>10.0 mm). Three to five small melanophores appear at 9.0 mm scattered along the dorsal surface of the snout. On juveniles >10.0 mm, 8–12 small melanophores are scattered on the anterior portions of upper and lower lips.

Preanal body pigmentation includes dense peritoneal pigment which spreads ventrally in bands along the dorsolateral surface of the coelomic wall. The banding results from variations in size and spacing of discrete melanophores. Peritoneal pigmentation appears less distinct on largest juveniles due to an increase in overlying musculature. A pronounced melanophore occurs on the ventral surface anterior to the anus on all specimens <5.1 mm, and occasionally on those 5.1–6.3 mm, but is absent on individuals >6.3 mm.

A large stellate melanophore is present (on all specimens examined) internally on myomere 15, 16, or 17 above the posterior end of the anal fin near the ventral body margin (Figures 1A, B; 2A–C). Three to seven smaller melanophores develop anteroventrally to this spot along the bases of anal fin rays, appearing first on 4.7-mm larvae and occurring on all larger specimens (Figures 1C, 2). Posterior to the large internal melanophore, 1–4 melanophores occur on the ventral margin of specimens <7.0 mm. The number of melanophores present in this region is variable, tending to increase in number with body length, specimens >7.0 mm having 5–12.

A small melanophore appears on larvae 5.1–5.4 mm along the dorsal margin of myomere 21 or 22. Specimens >5.4 mm have 5–9 melanophores on the dorsal margin of the caudal peduncle (Figure 2B, C). At 4.9 mm, an internal melanophore appears dorsal to the point of notochord flexure and is present in all larger specimens examined (Figure 2A–C). An additional melanophore appeared anterior to this melanophore in two specimens, 8.7 and 10.5 mm long. Specimens with all principal caudal rays developed have 1–6 melanophores near the bases of the rays, usually on the lower 8 principal rays (Figure 2).

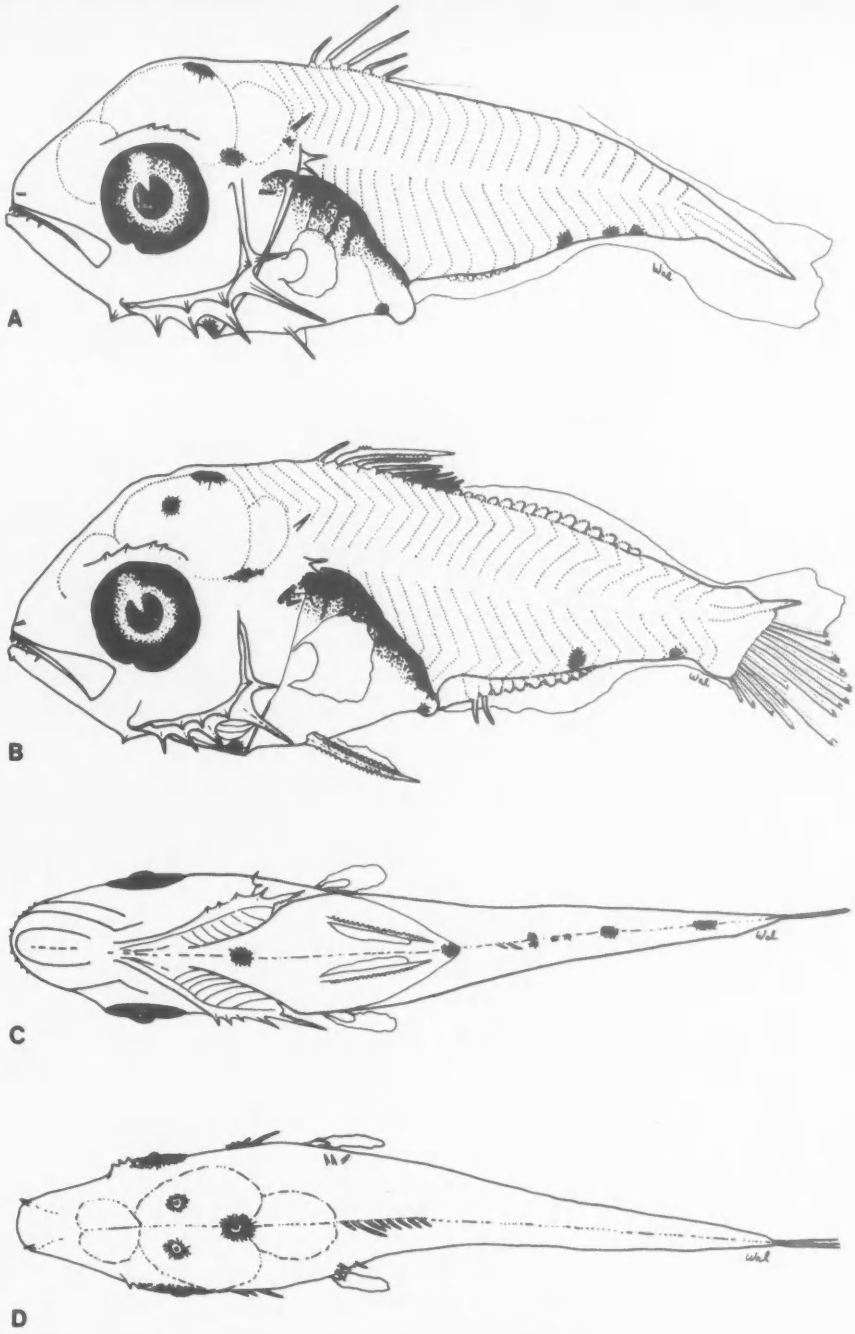

FIGURE 1.—Developmental stages of *Rhomboplites aurorubens:* A. 4.0-mm larva; B. 4.7-mm larva; C. 4.7-mm larva, ventral view; D. 4.7-mm larva, dorsal view.

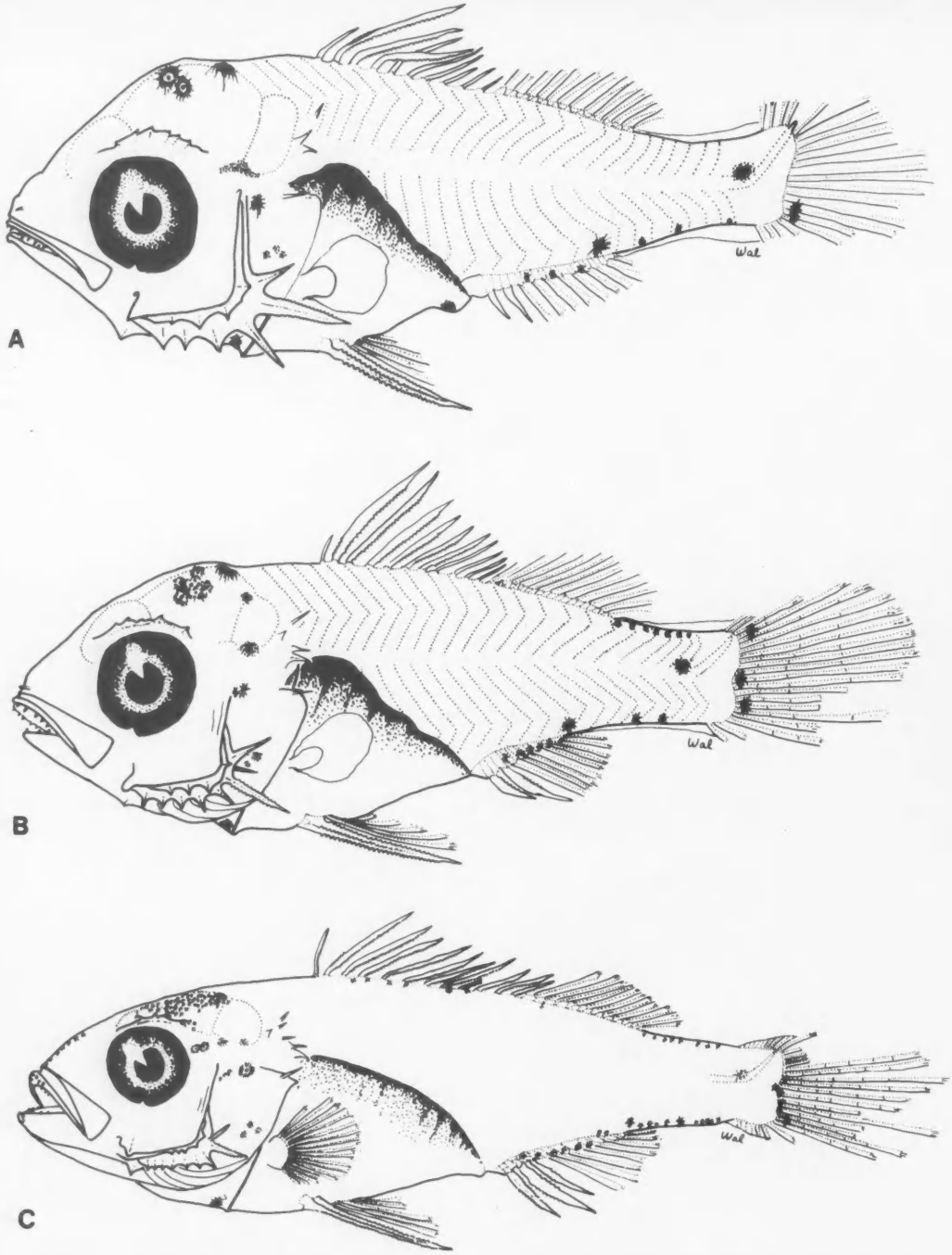

FIGURE 2.—Developmental stages of *Rhomboplites aurorubens:* A. 5.1-mm larva; B. 6.9-mm larva; C. 14.2-mm juvenile.

Fin Formation

Dorsal and pelvic fin formation begins by 4.0 mm (Figure 1A). Other fin development initiates in the following sequence: caudal, anal, and pectoral. The pelvic fins are first to complete development, while the dorsal fin is last.

Dorsal Fin

The anterior five dorsal spines are present on the smallest larva (4.0 mm) with an undifferentiated fin fold continuing to the caudal region (Figure 1A). The fin develops from anterior to posterior. At 4.8 mm, the adult number of dorsal fin elements appears with the posterior 1–3 spinous dorsal elements represented by soft rays.

Development of the dorsal fin occurs rapidly between 4.0 and 4.8 mm. After the adult number of fin-ray elements (23) appears, development towards the final adult dorsal fin complement (XII, 11) proceeds slowly as spines form from soft rays immediately posterior to the posteriormost spine. Dorsal spine development is similar to that described by Mansueti (1958) for anal spine development in *Roccus saxatilis*.

The dorsal fin is the last fin to attain the adult complement of spines and rays. Attainment of full dorsal fin complement between 8.3 and 10.9 mm marks the division between larval and juvenile stages.

The fourth dorsal spine is longest in adult *Rhomboplites aurorubens* (Jordan and Evermann 1898). The second dorsal spine is longest in all specimens of my series except the largest juvenile (14.2 mm) in which the third spine is longest (Figure 2C). The longest dorsal spine is longer than the longest dorsal soft ray throughout the series.

Dorsal spines are V-shaped in cross section, with the V open posteriorly. The two posterior edges are serrated nearly to the tip, which is sharp and oval in cross section. On larger spines the anterior edge is sometimes serrate for a short distance above the base (Figures 1B, 2B, C). Specimens between 4.8 and 9.0 mm have 29–40 serrations along each posterior edge of the second dorsal spine; larger specimens have 42–45 serrations.

Pelvic Fins

Pelvic fin spines and fin folds compose the pelvic fins of the 4.0-mm larva (Figure 1A). The pelvic fin attains the adult complement of I spine and 5 rays between 4.7 and 4.8 mm. The pelvic spine is long and serrate, extending slightly beyond the anus (24% SL) at its longest (about time of dorsal fin completion). Small specimens have spines which are V-shaped in cross section with serrations along all three edges. Specimens >4.5 mm have a double row of serrations along the leading edge of the spines creating an almost trapezoidal appearance in cross section (Figure 2).

Caudal Fin

The adult caudal fin has 17 principal and 19–21 procurrent rays (Miller and Jorgenson 1973). Principal rays are divided into two groups with 9 rays above and 8 rays below the midline of the body.

Notochord flexure occurs between 4.8 and 4.9 mm (Table 1). Flexure probably results in a slight decrease in standard length because the angle of the flexed notochord shortens the horizontal distance from snout tip to end of notochord. As a result of flexure and individual variation in rate of development, larvae of equal length may be at various stages of development (Table 1).

The caudal fin starts to form at the beginning of notochord flexure, about 4.7 mm. Fifteen or sixteen principal rays form simultaneously, slightly below and ventral to the posteroventral margin of the notochord. As the notochord flexes, these rays become elevated into the terminal position. The remaining rays are added dorsally and ventrally until the adult principal ray number is attained at about 4.8 mm (Figures 1B, 2A).

Anal Fin

The adult fin ray complement for vermilion snappers is III spines and 8 soft rays. Initial anal fin formation occurs at 4.7 mm. Embryonic fin rays (actinotrichia) are visible on 4.8-mm larvae. True soft rays (lepidotrichia) begin to form by 4.9 mm. The fin ray count remains II, 8 until about 5.4 mm and then becomes II, 9 (Table 1). The posteriormost ray forms last. The adult complement (III, 8) appears at about 8.3 mm as the anteriormost soft ray transforms into a spine. Each spine becomes serrate along its posterior edge, larger spines having a few serrations along the base of the anterior edge. The second anal spine is longest throughout the series studied, but in adults the third spine is longer.

TABLE 1.—Development of meristic characters of larval and small juvenile vermilion snapper, *Rhomboplites aurorubens*.

SL (mm)	Principal caudal fin rays		Dorsal fin		Anal fin		Pectoral fin rays	Pelvic fin		Notochord flexure
	Upper	Lower	Spines	Rays	Spines	Rays		Spines	Rays	
4.00			V					I		straight
4.13			VI					I		straight
4.67	8	7	VIII					I		straight
4.80	8	8	IX		II	8		I	5	flexed
4.80	9	8	XI	12	II	7		I	5	straight
4.80	9	8	X	13	II	8		I	5	flexed
4.87	9	8	X	13	II	8		I	5	flexed
4.93	9	8	X	13	II	8		I	5	flexed
4.93	9	8	X	13	II	8		I	5	straight
5.07	9	8	VIII	15	II	8		I	5	flexed
5.07	9	8	X	13	II	8		I	5	flexed
5.07	9	8	IX	14	II	8		I	5	flexed
5.07	9	8	IX	14	II	8		I	5	flexed
5.13	9	8	XI	12	II	8		I	5	flexed
5.27	9	8	X	13	II	8		I	5	flexed
5.40	9	8	X	13	II	9		I	5	flexed
5.46	9	8	XI	12	II	9		I	5	flexed
5.46	9	8	X	13	II	9		I	5	flexed
6.06	9	8	X	13	II	9		I	5	flexed
6.13	9	8	XI	12	II	9		I	5	flexed
6.26	9	8	XI	12	II	9		I	5	flexed
6.33	9	8	XI	12	II	9		I	5	flexed
6.40	9	8	XI	12	II	9		I	5	flexed
6.53	9	8	XI	12	II	9		I	5	flexed
6.53	9	8	XI	12	II	9		I	5	flexed
6.53	9	8	XI	12	II	9		I	5	flexed
6.93	9	8	XI	12	II	9	16	I	5	flexed
7.80	9	8	XI	—	II	9	16	I	5	flexed
8.26	9	8	XII	11	III	8	16	I	5	flexed
8.60	9	8	XI	12	III	8	17	I	5	flexed
8.66	9	8	XII	11	III	8	17	I	5	flexed
9.00	9	8	XI	12	III	8	17	I	5	flexed
10.00	9	8	XI	12	III	8	17	I	5	flexed
10.53	9	8	XII	11	III	8	17	I	5	flexed
10.80	9	8	XII	11	III	8	17	I	5	flexed
10.93	9	8	XI	12	III	8	18	I	5	flexed
11.20	9	8	XII	11	III	8	17	I	5	flexed
14.20	9	8	XII	11	III	8	17	I	5	flexed

Pectoral Fins

The pectoral fins are the last to begin development, embryonic rays becoming visible at about 4.9 mm. Ray formation proceeds from dorsal to ventral. True rays begin to form at about 6.9 mm, the adult complement, 17–18 rays, appearing by 8.6 mm.

Pectoral fin rays were frayed and broken on many specimens (including the specimen in Figure 2C). Longest pectoral fin rays without obvious damage were 11.9–15.0% SL, having no obvious within range correlation with standard length.

Head

All larvae have one small spine projecting from the posterodorsal portion of the operculum. This spine is very small and difficult to locate on small specimens (Figures 1, 2).

The preopercle is armed with two rows of spines. The smaller spines are located proximally along the margin of the preopercular crest, and the larger spines occur distally along the preopercular margin (Figures 1, 2). Both preopercular crest and preopercular margin have an upper (ascending) and lower (horizontal) margin which form approximately right angles.

Specimens <5.0 mm have 2 or 3 spines along the lower margin and 1 spine on the upper margin of the preopercular crest. Larger specimens have 3 or 4 spines along the lower and 1 or 2 spines along the upper margins (Figures 1, 2). Spines increase in size towards the angle of the preopercular crest.

Three spines are present along the lower margin of the preopercular margin on specimens <4.0 mm, 4 spines on specimens 4.0–5.4 mm, 5 spines on specimens 5.4–9.0 mm, and 6 or 7 spines on specimens >9.0 mm. These spines increase in size towards the angle of the margin, larger spines being serrated on juvenile specimens. A large, stout, and serrate spine occurs at the preopercular angle in all specimens. Length of the angle spine was 6.5% SL on the smallest larva (4.0 mm). All

other specimens <8.0 mm had angle spines which were 10.1–14.6% SL, averaging 12.6%. Specimens >8.0 mm had angle spines which were 7.0–13.1% SL, averaging 9.7%. The largest juvenile (14.2 mm) had the smallest spine within this group (7.0%). One spine occurred on the upper margin of the preopercular margin of all specimens examined, with a smaller spine occasionally occurring between it and the angle spine (Figure 2B).

The posttemporal has 1 or 2 sharp spines projecting posterodorsally; the supracleithrum, 2–5 similar spines; the number of spines increasing with growth (Figures 1, 2). The supraocular crest has 2–7 serrations which increase in number with growth. A sharp projection which appears to be the anterior tip of the lachrymal bone projects anteriorly and slightly ventrally from each side of the snout on all specimens.

The eye is nearly circular and has a ventral cleft (Figures 1, 2).

Conical teeth are present on premaxillary and dentary of all specimens; vomerine and palatine teeth, on 14.2-mm specimen.

TABLE 2.—Measurements of body parts for larval and juvenile vermilion snapper, *Rhomboplites aurorubens*, in millimeters.

SL	Head length	Snout to anus	Depth	Eye diameter
4.00	1.53	2.00	1.32	0.52
4.13	1.69	2.23	1.42	0.60
4.67	1.90	2.67	1.65	0.62
4.80	1.92	2.53	1.65	0.68
4.80	2.13	2.93	1.85	0.75
4.80	1.92	2.80	1.82	0.68
4.87	2.03	2.73	1.75	0.70
4.93	2.20	2.97	1.88	0.75
4.93	1.87	2.93	1.88	0.70
5.07	2.11	2.93	1.82	0.72
5.07	2.13	2.93	1.84	0.72
5.07	2.26	3.13	1.82	—
5.07	2.00	2.87	1.85	0.70
5.13	2.13	3.00	1.88	0.72
5.27	2.21	3.20	1.85	—
5.40	2.26	3.20	2.00	0.75
5.46	2.21	3.27	1.92	0.78
5.46	2.24	3.20	2.08	0.80
6.06	2.52	3.60	2.08	0.85
6.13	2.55	3.53	2.18	0.85
6.26	2.52	3.73	2.30	0.90
6.33	2.65	3.77	2.20	0.90
6.40	2.55	3.87	2.28	0.91
6.53	2.83	4.00	2.38	0.92
6.53	2.68	4.13	2.20	0.90
6.53	2.65	4.00	2.50	0.88
6.93	2.78	4.33	2.40	0.95
7.80	3.12	5.06	2.60	1.05
8.26	3.27	5.33	2.67	1.12
8.60	3.07	5.27	2.93	1.15
8.66	3.33	5.47	2.93	1.12
9.00	3.40	5.60	2.93	1.12
10.00	3.53	6.13	3.20	1.30
10.53	3.73	6.73	3.47	1.35
10.93	4.00	6.73	3.47	1.35
11.20	3.93	7.00	3.53	1.40
14.20	4.93	8.46	4.00	1.48

Body Growth

Measurements of body parts is presented in Table 2. The growth of various body parts as related to standard length is described by linear regression analysis using Bartlett's three-group method for Model II regression (Sokal and Rohlf 1969). Statistics for regressions of head length, depth of body, snout to anus distance, and eye diameter versus standard length are presented in Table 3. Correlation coefficients are greater than 0.97 for all relationships.

TABLE 3.—Statistics describing regressions of body measurements versus standard length for larval and small juvenile vermilion snapper, *Rhomboplites aurorubens*. The x variable is standard length in all cases.[1]

Variable y	Size range (mm)	$\bar{x}$	$\bar{y}$	N	b	a	$S_{y \cdot x}$	r
Head length	4.00–14.20	6.64	2.62	37	0.326	0.454	0.217	0.988
Body depth	4.00–14.20	6.64	2.28	37	0.285	0.388	0.198	0.986
Snout to anus	4.00–14.20	6.64	4.01	37	0.672	−0.450	0.185	0.995
Eye diameter	4.00–14.20	6.73	0.91	35	0.110	0.170	0.090	0.978

[1] $\bar{x}$ = mean value of x, $\bar{y}$ = mean value of y, N = number of specimens examined, b = rate of increase of y with respect to x, a = regression line intercept, $S_{y \cdot x}$ = standard deviation from the regression, r = correlation coefficient.

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SHORT-TERM THERMAL RESISTANCE OF ZOEAE OF 10 SPECIES OF CRABS FROM PUGET SOUND, WASHINGTON

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ABSTRACT

Zoeae of 10 crab species were subjected to tests that simulated thermal stress associated with steam-powered electric stations. Shortly after hatching, the unfed zoeae were subjected to conditions simulating passage through heat exchangers (held at elevated test temperatures for 20 min with an abrupt increase and decrease from ambient) or mixing with thermal plumes (held at test temperature 1 to 4 h with temperatures gradually rising and decreasing from ambient). All species used in tests were hatched from February to November and were naturally acclimated to ambient conditions of the littoral zone. Observations were made on the point in temperature that zoeae became torpid in heat exchanger tests and on the TL_{50} (maximum temperature–time that 50% or more of the subjects survived 48 h after testing).

In the heat exchanger tests, the most sensitive species, the Bering hermit crab, *Pagurus beringanus*, and the porcelain crab, *Petrolisthes eriomerus*, did not become torpid at 24°C; their torpid point and their TL_{50} were at 26°C. The economically important Dungeness crab, *Cancer magister*, did not become torpid at 28°C; its TL_{50} was at 30°C. The TL_{50} of other species ranged from 30° to 34°C.

The TL_{50} of zoeae given the thermal plume test ranged from 26° to 34°C for a 1-h exposure and 24° to 32°C for a 2- to 4-h exposure.

Thermal conditions in heat exchangers are postulated to be more critical to the survival of zoea than mixing with thermal plumes. The maximum temperature that should be permitted in heat exchangers to protect the most sensitive species studied is 24°C for the Puget Sound area.

Thermal resistance of marine organisms should be understood before seawater in a specific area is used for industrial cooling. In the State of Washington, for example, nuclear power plants are being planned for construction by municipalities and industries. These plants require large quantities of seawater to cool condensers of the steam turbine system; their waste hot water would be discharged back into the environment, along with toxic chemicals (Becker and Thatcher[2]). Organisms entrained into steam electric stations would be subjected to mechanical injury (Marcy 1973) from passage through such a system. Studies are needed to fully evaluate the impact of entrainment and the discharge of altered waste water on the associated life; temperature effects are considered here.

Some information is available on the thermal maximums and optimums of two species of Puget Sound crabs (Todd and Dehnel 1960; Reed 1969; Prentice 1971; Mayer[3,4]). These studies show the effects of long-term temperature increases but do not depict situations related to industrial use of seawater for cooling. Experiments reported here were designed to simulate the stress that zoeae would be exposed to in passing through heat exchangers of steam electric stations and in mixing with thermal plumes of the waste water released into the environment.

This study is one of a series describing the thermal resistance of selected species of planktonic organisms. The time-temperature combinations used are considered a measure of thermal resistance (Fry 1971) because they are probably beyond the environmental tolerance of the species used. This paper describes the elevated temperatures that cause immediate and imminent

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death and stress to the zoeae of four species of anomuran and six species of brachyuran crabs acclimatized to natural ambient conditions. These crabs constitute some of the more important types in the littoral zone and include species important in sport and commercial fisheries. Testing was done at the National Marine Fisheries Service facility at Mukilteo, Wash., from May to October 1971 and in February 1972.

MATERIALS AND METHODS

Ovigerous crabs were collected from the mid-Puget Sound areas of Possession Sound, Poverty Bay, and at Alki Point. Graceful crab, *Cancer gracilis*, Dungeness crab, *C. magister*, and kelp crab, *Pugettia producta*, were collected subtidally; other species were taken on beaches during low tides. The messmate crab, *Pinnixa littoralis*, was collected inside horse clam, *Tresus capax*, that had been excavated. Most of the experimental species were ovigerous in May and June; the mud flat crab, *Hemigrapsus oregonensis*, black clawed crab, *Lophopanopeus bellus*, and porcelain crab, *Petrolisthes eriomerus*, had ovigerous individuals to August. *Pugettia producta* were ovigerous July to November.

Ovigerous crabs and pre- and posttest zoeae were held in aquaria receiving running seawater of temperatures ranging from 8.2° to 23.5°C (Table 1); salinity ranged from 24.1 to 28.3‰; and dissolved oxygen ranged from 5.6 to 9.0 ppm. Laboratory water was sometimes 3°C higher than ambient temperatures at the surface in the afternoon on sunny days in July and August because of heating of the water supply pipe. Other than this, the ambient water temperatures of the Mukilteo area were similar to that expected of central Puget Sound locations (Wennekens 1959).

TABLE 1.—Temperature of Mukilteo, Wash., laboratory seawater summarized by 10-day periods in 1972.

	Water temperature (°C)		
	Average		
Month	Low	High	Range
May	9.3	10.0	8.2–10.7
	9.9	10.4	9.1–11.1
	9.5	11.4	8.8–12.7
June	10.4	12.2	10.0–13.3
	10.4	12.7	9.7–14.3
	10.8	13.5	10.4–14.3
July	11.0	13.1	10.4–14.0
	—	—	—
	12.3	16.4	11.3–18.2
August	12.9	16.4	11.3–18.2
	16.6	20.7	13.5–23.5
	15.7	18.6	13.0–23.0
September	13.2	14.9	12.6–15.6
	12.9	15.5	12.5–16.8
	13.7	15.9	12.5–16.8

Test facilities consisted of floating holding boxes for test groups of zoeae and 5-liter battery jars for maintaining water baths of a controlled temperature. Holding boxes were 2.5 cm^3, with two screened sides having 0.110-mm apertures, attached to Styrofoam[5] for floatation. Battery jars received 3 liters of seawater immediately before testing. Temperatures were maintained within ±0.5°C of the test temperatures during experiments. Continuous aeration insured mixing and oxygenation.

Zoeae generally hatched within a week after their parents were collected, but some parents were held a month before hatching occurred. When the zoeae hatched (hatching of all ova of a parent occurred within about 12 h), 10 were counted into each of the holding boxes within 24 h of hatching and remained there, unfed, to the termination of an experiment. Zoeae used as controls were held at the temperature of laboratory water, and others were given two types of thermal tests.

To simulate passage through heat exchangers, holding boxes containing 10 zoeae were removed from water of ambient temperature and placed directly into battery jars having water of an elevated temperature ranging from 24° to 38°C by 2°C increments (Table 2). The zoeae remained at the elevated temperature for 20 min and were then placed into water of ambient temperature. Actual temperature change within the holding boxes was delayed. On the average, the increase from ambient to midway to the test level occurred in 5 s. Temperatures were within 1°C of the test level in 2 min. Decreases from test temperatures to ambient occurred in about 1½ min. Activity of zoeae was noted before, during, and after testing.

To simulate conditions encountered in thermal plumes, zoeae in holding boxes were placed in water of ambient temperature in the battery jar. The temperature of the water was then elevated to a test temperature ranging from 24° to 36°C by 2°C increments (Table 2) over a 30-min period. Specific groups of zoeae were held at specific test temperatures for durations of 1, 2, or 4 h. After this, the temperature was gradually decreased to ambient level over a 20-min period, and the

[5]Reference to trade name does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Percentage survival of first stage zoeae 48 h after testing of 10 species of crabs subjected to a range of temperatures at four durations (percentages are from combined data of two or more tests). Increases to and decreases from a test temperature were rapid for the 20-min test (heat exchanger test) and gradual for the longer durations of exposure (thermal plume test).

Species	Minutes held at test temperature	Date at end of test	No. of parents	Control: No. zoeae	Control: Percent survival	No. zoeae tested	Survival at different water temperatures (°C): 24°	26°	28°	30°	32°	34°	36°	38°
							Percentage							
Anomuran:														
Bering hermit crab,	20	6/20	2	60	53	30	80	[1]*55*	47	0	0	—	—	—
Pagurus beringanus	60	7/28					55	*73*	37	10	0	—	—	—
	120						*50*	30	0	17	0	—	—	—
	240						*65*	37	3	0	0	—	—	—
Granular hermit crab,	20	6/25	3	90	92	30	—	87	83	*70*	0	0	—	—
Pagurus granosimanus	60	6/27					—	93	80	*77*	0	0	—	—
	120	7/2					—	90	90	*53*	0	0	—	—
	240						—	90	*83*	23	0	0	—	—
Hairy hermit crab,	20	6/5	3	80	93	10-30	—	80	80	*53*	10	7	0	—
Pagurus hirsutiusculus	60	6/13					—	100	77	*85*	37	0	0	—
	120	6/23					—	*100*	80	*80*	30	0	—	—
	240						—	*80*	83	*65*	7	0	0	—
Porcelain crab,	20	6/23	3	40	83	10-30	—	45	30	0	0	—	—	—
Petrolisthes eriomerus	60	6/25					—	70	*50*	0	0	—	—	—
	120	7/2					—	*100*	0	0	0	—	—	—
	240						—	*80*	0	0	0	—	—	—
Brachyuran:														
Black clawed crab,	20	6/16	3	100	89	40	100	98	90	95	*63*	13	0	—
Lophopanopeus bellus	60	6/23					100	98	98	*85*	5	3	—	—
	120	9/16					90	100	98	*75*	8	0	—	—
	240						80	98	83	*55*	0	3	—	—
Dungeness crab,	20	6/7	4	60	93	50	100	90	80	*78*	14	0	—	—
Cancer magister	60	6/9					100	94	*74*	18	6	0	—	—
	120	6/28					100	96	*90*	0	0	0	—	—
	240	2/29/72					100	94	*62*	2	0	0	—	—
Graceful crab,	20	7/16	2	60	95	40	88	90	90	*88*	23	0	—	—
Cancer gracilis	60	7/18					93	90	*90*	25	0	0	—	—
	120						90	83	*93*	3	0	0	—	—
	240						93	85	*80*	0	0	0	—	—
Kelp crab,	20	9/2	2	80	100	40	—	100	100	100	*90*	10	0	—
Pugettia producta	60	10/15					—	98	100	98	*88*	0	0	—
	120						—	98	90	*93*	13	0	0	—
	240						—	95	*95*	30	0	0	0	—
Messmate crab,	20	7/30	2	80	95	40	90	83	85	*83*	25	0	—	—
Pinnixa littoralis	60	8/4					95	98	88	*60*	3	0	—	—
	120						83	85	*95*	30	0	0	—	—
	240						93	93	*63*	13	0	0	—	—
Mud flat crab,	20	6/13	5	130	98	20-50	—	100	100	100	92	*52*	0	0
Hemigrapsus oregonensis	60	6/18					—	97	98	96	94	*54*	10	—
	120	7/2					—	100	100	100	*100*	46	0	—
	240	7/8					—	100	90	100	*98*	48	0	—
		8/28												

[1]Italic denotes the TL_{50}.

holding boxes containing zoeae were replaced in aquaria with running seawater.

The numbers of replicate tests made at a temperature for a test varied because of numbers of ovigerous crabs available and numbers of zoeae resulting from a hatching. The offspring from at least two parent crabs of a species were used (Table 2). Some species were tested at intervals over a 2- to 3-mo period to indicate seasonal acclimation effects. One test for *C. magister* was made in 1972; all other species were tested in 1971. Percentage survival of a species of crab for a given duration and temperature is the combined survival of two to five tests made for a species (Table 2).

Observations were made on the levels of activity, point of torpor, and the TL_{50} (maximum temperature–time combination survived by 50% or more of subjects 48 h after testing) to evaluate the effects of experimental conditions. A 48-h posttest observation duration was deemed appropriate for these tests as the zoeae were not fed and could have been affected by starvation although they readily survived to 72 h.

TEMPERATURE EFFECTS

Temperature–time combinations for a type of test that was critical to the survival of the zoeae of a species were indicated by survival of the controls and by experimental conditions affecting activity and survival of the test subjects.

Zoeae used as controls had survival rates ranging from 53 to 100% (Table 2). Guidelines set in the American Public Health Association (1971) state that losses of greater than 10% of control subjects invalidate an experiment. Control zoeae of the Bering hermit crab, *Pagurus beringanus*, with a survival of 53%, *L. bellus* with a survival of 89%, and *Petrolisthes eriomerus*, with a survival of 83% fall below this standard. Although the TL_{50}'s are invalid for these species, the point of torpor is valid as it demonstrates an immediate condition the zoeae lapse into with a given temperature stress.

Activity and survival of a species of zoeae decreased with increasing temperature and duration at an elevated test temperature (Table 2). In heat exchanger tests, zoeae experienced a rapid temperature change and were initially hyperactive, probably as a result of thermal shock (Kinne 1964). With time, zoeae at a temperature 4°C below the TL_{50} appeared normal. Those at 2°C below TL_{50} had reduced activity and had difficulty maintaining themselves off the bottom. Subjects placed in water at the TL_{50} temperature and above were initially hyperactive, but in 2 to 7 min became torpid and sank to the bottom. Heat exchanger test temperatures producing torpor were 26°C for *Pagurus beringanus* and *Petrolisthes eriomerus* and 30°C for most other test species; the maximum was 32°C for *L. bellus*, *Pugettia producta*, and *H. oregonensis*. After the zoeae were returned to ambient conditions, those tested at the TL_{50} temperature had not become active after 20 min.

Zoeae subjected to the heat exchanger tests generally had high survival to the point of the TL_{50} (Table 2). Thereafter, mortalities were complete at 2° to 4°C higher except in the case of the hairy hermit crab, *Pagurus hirsutiusculus*, where all died at 6°C above the TL_{50}. The minimal TL_{50} was at 28° and 30°C for most other crabs; it was at 32°C for *Pugettia producta* and *L. bellus* (Table 2). The most tolerant species was *H. oregonensis* with a TL_{50} at 34°C.

Zoeae subjected to the thermal plume tests had lower TL_{50}'s than those given the heat exchanger tests (Table 2). The TL_{50} of zoeae given the 60-min test was similar to or 2°C lower than those given the 20-min heat exchanger test; TL_{50}'s were at progressively lower temperatures for the 120- and 240-min tests. Mortalities were complete at 2° to 4°C above the TL_{50}. The least tolerant species were the *Cancer* crabs (Table 2) with TL_{50}'s at 28°C for the 60- and 240-min tests. TL_{50}'s were generally at 30°C for the other crabs for the three time durations they were tested. The species with the highest tolerance was *H. oregonensis* with a TL_{50} at 34°C for the 60-min test and at 32°C for the 120- and 240-min tests.

DISCUSSION

The situation postulated to be most critical to the survival of the planktonic zoeae is their passage through heat exchangers; zoeae will be entrained into heat exchanger systems but those encountering thermal plumes will probably only be exposed to lowering temperatures (Coutant 1970) at the periphery where turbulence occurs.

The maximum temperature limit that should occur in heat exchangers is best described as the one causing no adverse effects to the least resistant species—to be consistent with the protection of all species tested. Conditions that could be overtly recognized as affecting the survival of the zoeae were the degree of stress causing torpor and the TL_{50}. While the TL_{50} directly relates to death, torpor indicates a condition that could indirectly cause death. Torpid zoeae would have their feeding interrupted and they would not be able to evade predators until they recovered. Selective predation on zoeae subjected to a stress below that causing torpor could also be a factor of survival at sublethal temperature–time combinations. In fish, for example, Coutant (1973) experimentally observed that rainbow trout, *Salmo gairdneri*, predators selectively preyed on juvenile rainbow trout and chinook salmon, *Oncorhynchus tshawytscha*, that had been exposed to shock temperature treatments of durations below that required for the prey to lose equilibrium.

The maximum temperature that had no observable effect on the species studied was 24°C, as this was the greatest stress that did not cause *Pagurus beringanus* and *Petrolisthes eriomerus* to become torpid. The maximum for other species should be no greater than 28°C for *Cancer* and up to 30° to 32°C for the most resistant species.

A properly sited steam electric station should not discharge hot waste water in quantities or at locations where thermal plumes would retain their integrity over periods of 1 to 4 h. This could be a problem if Puget Sound waters were intensively used for cooling. TL_{50}'s for the zoea subjected to the 1- to 4-h thermal plume test

ranged from 28° to 32°C, except that *H. oregonensis* had a TL_{50} of 34°C for the 1-h test.

The maximum temperature increase in a steam electric station that will not cause mortality to the species studied can be estimated from the seawater temperature in Puget Sound and the maximum temperatures tolerated by zoeae. Surface temperatures of Puget Sound range from about 10°C in the spring when most zoeae hatch to 15°C or more in some locations in the summer (Wennekens 1959). Temperatures in heat exchangers can be increased 14°C in the spring and 9°C in the summer without causing direct or indirect mortalities to the least resistant species. Synergistic effects from the release of toxic chemicals and from mechanical damage may act to lower the thermal maximums tolerated.

Knowledge of the temperature tolerance of the zoeae studied provides a partial input into the assessment of the impact of a steam electric station using Puget Sound waters for cooling. Zoeae are generally a minor component of zooplankton within the depths of Puget Sound that would be subject to entrainment (Hebard 1956; Patten unpubl. data). Also, the volume of water entrained by a steam electric station would be small in comparison to that of Puget Sound. Therefore, if all entrained zoeae were destroyed in a steam electric station, the proportion lost may be of minor concern on the population level. Losses of zoeae from high temperature conditions may be more serious if a series of steam electric stations used Puget Sound waters for cooling. In this case, some conservation measures should be considered.

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A SIMPLIFICATION FOR THE STUDY OF FISH POPULATIONS BY CAPTURE DATA

SAMIR Z. RAFAIL[1]

ABSTRACT

Expressions given by Rafail for estimating catchability are modified here to eliminate iteration, for better accuracy, and a large economy in calculations and time. The evaluation of catchability allows the estimation of other important parameters with the useful assumption of their variabilities according to seasons and recognized sections of a population.

The evaluation of some parameters of fish populations from capture data began at the start of the century (Edser 1908; Heincke 1913; Baranov 1918). Beverton and Holt (1957) derived an equation in two forms (equations (14.19) and (14.86)) for the estimation of catchability and natural mortality from catch and effort data for a whole series of years assuming identical survival rates and catchabilities for all ages in a given year, fishing effort varies from year to year, and negligible recruitment and migrations.

Paloheimo (1961) modified the iteration method by Beverton and Holt (1957) to a simpler one without iteration using the relationship $(1 - e^{-i})/i \approx e^{-0.5i}$ where i is the instantaneous total mortality.

Allen (1966) described three methods for estimating a population and one for recruitment by using data on annual age composition, number caught, effort to take a known part of the catch assuming a constant recruitment rate all over a year, equal catchability for the different age groups, and available comparisons between exploited and unexploited populations with equal natural mortality. Allen (1968) described a simplification of his method for computing recruitment rates.

Among the investigators who studied the variability of parameters of fish populations, Gulland (1964) described variations in catchability as cyclical, long-term trends due to amount of fishing and changes in abundance, diurnal changes due to feeding and light, temperature like severe winters, and sex. Paloheimo and Kohler (1968) concluded from their analysis of a cod population that catchability and natural mortality showed variations associated with age and years. Walker (1970) gave evidence of increased natural mortality with age due to senescence for cod.

Rafail (1974) recognized the probable great variability of parameters of fish populations and derived expressions for the evaluation of catchability, fishing mortality, natural mortality, and recruitment assuming their variability from one season to another and their constancy during the seasons as well as their variation from a recognized section of a population to another like age-groups and different sexes. His equations for the evaluation of catchability as the first parameter to be estimated require a number of iterations which may be relatively very large if recruitments exceed the sum of natural and fishing mortalities. Therefore, a computer is needed for accurate calculations and this is a disadvantage.

The present treatment transforms the equations given by Rafail (1974) to estimate catchability into forms that dispense with iterations and yield more accurate estimates.

SAMPLING PROCEDURE

A fish population with a certain initial size is distributed on a constant area and subjected to a sequence of sampling surveys which can be grouped into a number of groups. Each group of surveys must contain at least three sampling surveys. The parameters of the population are assumed to vary among the groups of surveys and remain constant within each group which represents a season with constant properties. The entire fishing fleet may be considered as sampling

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vessels whose catch data are to be collected adequately.

If the fleet is large, a part of the fleet is appointed as sampling vessels while the effective fishing effort of unappointed vessels should be estimated. The sampling surveys should follow one another with no intervening time periods within a group of surveys. The durations of the surveys may vary from one survey to another or kept constant if the total fishing effort varys from survey to survey. The total effort exerted on the population should vary from one survey to another.

ASSUMPTIONS

1. A fish population has a constant area of distribution and a constant uniform distribution of fishing relative to fish concentration so that the instantaneous fishing mortality is proportional to fishing effort.

2. The population is subjected to a sequence of n sampling surveys grouped into M groups representing M seasons with constant population parameters. The duration of the kth survey is denoted by T_k. The catchability or percentage of available fish captured by a standard unit of fishing effort during the kth survey is denoted by q_k.

3. The commercial and sampling vessels exert a constant fishing effort per unit time during the kth survey denoted by f_{kc} and f_{ks} respectively, so that the efforts exerted become

$$f_{ks} \cdot T_k = f'_{ks} \quad (1.1)$$
$$f_{kc} \cdot T_k = f'_{kc} \quad (1.2)$$
$$f_{ks} + f_{kc} = f_k \quad (1.3)$$
$$f'_{ks} + f'_{kc} = f'_k \quad (1.4)$$

where f'_{ks}, f'_{kc}, and f'_k represent the total fishing effort exerted by the sampling, commercial vessels, and the whole fleet, respectively, during the kth survey.

4. The instantaneous fishing mortalities per unit time by the sampling, commercial, and total fleet in the kth survey are denoted by F_{ks}, F_{kc}, and F_k, respectively. The instantaneous fishing mortalities during the kth survey (F'_{ks}, F'_{kc}, and F'_k) are evaluated as

$$F_{ks} \cdot T_k = F'_{ks} = q_k \cdot f'_{ks} \quad (1.5)$$
$$F_{kc} \cdot T_k = F'_{kc} = q_k \cdot f'_{kc} \quad (1.6)$$
$$F_k \cdot T_k = F'_k = q_k \cdot f'_k. \quad (1.7)$$

5. The fish population has an initial size denoted by N_0. The number of fish present at the start of the kth survey is N_{k0} while the number of fish present at the end of the kth survey or the start of the $(k+1)$th survey is $N_{(k+1)0}$.

6. The instantaneous natural mortality rate per unit time during the kth survey is M_k. The instantaneous natural mortality during the kth survey is

$$M_k \cdot T_k = M'_k. \quad (1.8)$$

7. The instantaneous recruitment rate per unit time during the kth survey relative to the number of fish present is R_k. The number of fish present at the end of the kth survey or the start of the $(k+1)$th survey when recruitment is acting solely is

$$N_{(k+1)0} = N_{k0} \cdot \exp(R_k \cdot T_k) = N_{k0} \cdot \exp(R'_k), \quad (1.9)$$

that is,

$$R_k \cdot T_k = R'_k, \quad (1.10)$$

where R'_k denotes the instantaneous recruitment rate during the kth survey.

8. The instantaneous rate of change of fish abundance per unit time during the kth survey relative to the number of fish present is "A_k" which is the "instantaneous abundance coefficient" so that

$$N_{(k+1)0} = N_{k0} \cdot \exp(A_k \cdot T_k) = N_{k0} \cdot \exp(A'_k). \quad (1.11)$$

In other words, $A_k \cdot T_k = A'_k$ and A'_k denotes the instantaneous change of abundance during the kth survey.

According to previous assumptions we have

$$A'_k = R'_k - M'_k - F'_k = (R_k - M_k - F_k)T_k \quad (1.12)$$

and

$$N_{(k+1)0} = N_{k0} \cdot \exp(A'_k) = N_{k0} \cdot \exp(R'_k - M'_k - F'_k). \quad (1.13)$$

9. If the sampling surveys $(k-1)$, k, and $(k+1)$ belong to the same season,

$$R_{k-1} = R_k = R_{k+1} = \bar{R}_k \quad (1.14)$$
$$M_{k-1} = M_k = M_{k+1} = \bar{M}_k \quad (1.15)$$

and

$$q_{k-1} = q_k = q_{k+1} = \bar{q}_k \qquad (1.16)$$

where $\bar{R}_k$, $\bar{M}_k$, and $\bar{q}_k$ are constant parameters per unit time during the $(k-1)$th, kth, and $(k+1)$th sampling surveys which should belong to the same season.

$$\therefore \qquad \bar{R}_k - \bar{M}_k = \bar{B}_k \text{ (a constant).} \qquad (1.17)$$

10. If $T_k = T_{k-1} = T_{k+1}$ and similar to Equations (1.8), (1.10), and according to (1.17), we get

$$\bar{M}_k T_k = \bar{M}'_k,\ \bar{R}_k T_k = \bar{R}'_k, \text{ and } \bar{B}_k T_k = \bar{B}'_k \qquad (1.18)$$

where $\bar{M}'_k, \bar{R}'_k$, and $\bar{B}'_k$ represent the instantaneous rates of natural mortality, recruitment, and the difference between them during single surveys (not per unit time) belonging to the same season when the durations of the surveys are made equal.

11. The number of fish captured by the sampling, commercial, and the total fleet during the kth survey are denoted by C_{ks}, C_{kc}, and C_k, respectively.

12. The catch per unit efforts during the kth survey obtained from sampling, commercial, and total fleet are respectively

$$(C/f')_{ks},\ (C/f')_{kc}, \text{ and } (C/f')_k$$

where f is primed (f') according to previous notations to designate exerted effort during a whole sampling survey and not per unit time.

13. The following expressions are used to obtain simpler mathematical equations:

$$\big(\exp(A'_k) - 1\big)/A'_k = a_k \qquad (1.19)$$

$$a_k{}^2/a_{k-1} \cdot a_{k+1} = a'_k \qquad (1.20)$$

$$(C/f')_k{}^2/(C/f')_{k-1} \cdot (C/f')_{k+1} = (C/f)'_k. \qquad (1.21)$$

A MODIFICATION FOR THE EXPRESSION ESTIMATING CATCHABILITY

Rafail (1974) developed an estimate for $\bar{q}_k$ according to his equation (4.16) briefly as follows when the whole fleet is engaged for sampling:

$$C_k = N_0 \cdot \exp\Big(\sum_{j=1}^{k-1} A'_j\Big) \cdot F'_k \cdot a_k \qquad (2.1)$$

and

$$C_{k+1} = N_0 \cdot \exp\Big(\sum_{j=1}^{k} A'_j\Big) \cdot F'_{k+1} \cdot a_{k+1} \qquad (2.2)$$

$$\therefore \qquad \frac{C_{k+1}}{C_k} = \exp(A'_k) \cdot \frac{a_{k+1}}{a_k} \cdot \frac{F'_{k+1}}{F'_k} \qquad (2.3)$$

and

$$\frac{C_k}{C_{k-1}} = \exp(A'_{k-1}) \cdot \frac{a_k}{a_{k-1}} \cdot \frac{F'_k}{F'_{k-1}} \qquad (2.4)$$

and

$$\frac{C_k{}^2}{C_{k-1} \cdot C_{k+1}} = \frac{\exp(A'_{k-1})}{\exp(A'_k)} \cdot \frac{a_k{}^2}{a_{k-1} \cdot a_{k+1}} \cdot \frac{F'^2_k}{F'_{k-1} \cdot F'_{k+1}}. \qquad (2.5)$$

According to Equations (1.7) and (1.16) we get

$$\frac{F'^2_k}{F'_{k-1} \cdot F'_{k+1}} = \frac{\bar{q}_k{}^2 \cdot f'^2_k}{\bar{q}_k{}^2 \cdot f'_{k-1} \cdot f'_{k+1}} = \frac{f'^2_k}{f'_{k-1} \cdot f'_{k+1}}. \qquad (2.6)$$

As we have $\dfrac{\exp(A'_{k-1})}{\exp(A'_k)} = \exp(A'_{k-1} - A'_k)$ and according to Equation (1.12), we get

$$\exp(A'_{k-1} - A'_k) = \exp\big((R_{k-1} - M_{k-1} - F_{k-1})T_{k-1} - (R_k - M_k - F_k)T_k\big).$$

Again according to Equations (1.14) and (1.15), as well as (1.7) and (1.16), we get

$$\exp(A'_{k-1} - A'_k) = \exp\big((\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \bar{q}_k(f'_{k-1} - f'_k)\big). \qquad (2.7)$$

From Equations (1.20), (2.5), (2.6), and (2.7) we get

$$\frac{C_k{}^2}{C_{k-1} \cdot C_{k+1}} = \exp\big((\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \bar{q}_k(f'_{k-1} - f'_k)\big) \cdot a'_k \cdot \frac{f'^2_k}{f'_{k-1} \cdot f'_{k+1}}.$$

Rearranging and according to assumption 12 we get

$$\frac{(C/f')_k{}^2}{(C/f')_{k-1} \cdot (C/f')_{k+1}} = \exp\big((\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \bar{q}_k(f'_{k-1} - f'_k)\big) \cdot a_k.$$

Using Equation (1.21), the above equation is transformed to

$$\bar{q}_k = \frac{\log_e(a'_k) + (\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \log_e(C/f)'_k}{f'_{k-1} - f'_k}. \quad (2.8)$$

If sampling surveys are arranged to have equal durations (or $T_{k-1} = T_k = T_{k+1}$), then Equation (2.8) reduces to

$$\bar{q}_k = \frac{\log_e(a'_k) - \log_e(C/f)'_k}{f'_{k-1} - f'_k}. \quad (2.9)$$

Equations (2.8) and (2.9) will be modified if a part of the commercial fleet is engaged with the sampling surveys so that $(C/f)'_k$ will be replaced by $(C/f)'_{ks}$, so that the last expression will be evaluated from the catch per unit effort of the sampling vessels "$(C/f')_{ks}$ of assumption 12," while all other items will remain the same.

Again it is important to note that the data of three successive surveys should be used to obtain a single q-estimate because in case of unsuccessive data the fraction $\exp(A'_{k-1})/\exp(A'_k)$ of Equation (2.5) will be biased and Equations (2.8) and (2.9) will not hold good.

Equations (2.8) and (2.9) can be used to estimate $\bar{q}_k$ by a number of iterations which is large when fish abundance is increasing and much fewer with decreasing abundance (Rafail 1974).

The modification of Equations (2.8) and (2.9) is based on the fact that a_k shown by Equation (1.19) can be evaluated as a function of A'_k. Paloheimo (1961) gave the following approximation:

$$a_k = \left(1 - \exp(-A')\right)/A' \approx \exp(-0.5A'). \quad (3.1)$$

Rafail (1974) has shown that when the instantaneous rate of change of fish abundance is negative, then a_k of Equation (1.19) can be represented as in Equation (3.1). In fact a_k is more precisely expressed as

$$a_k \approx \exp(\alpha_1 A'_k + \alpha_2 A'^2_k + \alpha_3 A'^3_k) \quad (3.2)$$

where α_1, α_2, and α_3 denote certain constants. A simpler and sufficient precise expression for a_k is fitted here as

$$a_k \approx \exp(\pm 0.5A'_k + 0.04A'^2_k). \quad (3.3)$$

Table 1 shows a comparison between the values of a_k calculated by the exact Equation (1.19) and those calculated by Equation (3.3).

TABLE 1.—A comparison between a_k-values calculated according to the exact Equations (1.19) and (3.3).

A'	$\exp(A')$	$a = (\exp(A') - 1)/A'$	$x = \pm 0.5A' + 0.04A'^2$	$a = \exp(x)$
−0.02	0.9802	0.9901	−0.01	0.9900
−0.10	0.9048	0.9516	−0.0496	0.9516
−0.20	0.8187	0.9063	−0.0984	0.9063
−0.50	0.6065	0.7869	−0.2400	0.7866
−1.00	0.3679	0.6321	−0.4600	0.6313
−2.00	0.1353	0.4323	−0.8400	0.4317
−2.25	0.1054	0.3976	−0.9225	0.3975
−2.50	0.0821	0.3672	−1.00	0.3679
−2.65	0.0707	0.3507	−1.0441	0.3520
−2.75	0.0639	0.3404	−1.0725	0.3421
−3.00	0.0498	0.3167	−1.14	0.3198
0.02	1.0202	1.0100	0.010016	1.0107
0.10	1.1053	1.0530	0.05040	1.0517
0.20	1.2215	1.1075	0.10160	1.1070
0.50	1.6486	1.2972	0.26000	1.2968
1.00	2.7184	1.7184	0.54000	1.7160
2.00	7.3890	3.1945	1.16000	3.1900
2.25	9.4877	3.7723	1.32750	3.7716
2.50	12.1828	4.4731	1.50000	4.4817
2.65	14.1544	4.9639	1.60590	4.9823
2.75	15.6428	5.3246	1.67750	5.3521
3.00	20.087	6.3623	1.86000	6.4237

Table 1 shows that Equation (3.3) can be used to calculate a_k with a maximum error less than 1% when A' lies between ±3.00, i.e., an error which is practically negligible. Again, the smaller the value of A' the smaller is the error so that when A' lies between ±2.5, the error is less than 0.2%, and Equation (3.3) can be considered as a highly precise expression in that range which is always encountered in fisheries studies. Equation (3.3) can be used to evaluate a'_k given by Equation (1.20) as

$$a'_k = \frac{\left(\exp(\alpha_1 A'_k + \alpha_2 A'^2_k)\right)^2}{\exp(\alpha_1 A'_{k-1} + \alpha_2 A'^2_{k-1}) \cdot \exp(\alpha_1 A'_{k+1} + \alpha_2 A'^2_{k+1})}$$

and

$$\log_e a'_k = \alpha_1(2A'_k - A'_{k-1} - A'_{k+1}) + \alpha_2(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}). \quad (4.1)$$

According to Equations (1.12), (1.14), (1.15), and (1.16) we get

$$A'_k = (\bar{R}_k - \bar{M}_k)T_k - F'_k \quad (4.2)$$

$$\begin{aligned} \therefore 2A'_k - A'_{k-1} - A'_{k+1} &= 2T_k(\bar{R}_k - \bar{M}_k) - 2F'_k \\ &\quad - T_{k-1}(\bar{R}_k - \bar{M}_k) + F'_{k-1} \\ &\quad - T_{k+1}(\bar{R}_k - \bar{M}_k) + F'_{k+1} \\ &= (\bar{R}_k - \bar{M}_k)(2T_k - T_{k-1} - T_{k+1}) \\ &\quad - 2F'_k + F'_{k-1} + F'_{k+1} \end{aligned}$$

or

$$2A'_k - A'_{k-1} - A'_{k+1} = (\bar{R}_k - \bar{M}_k)(2T_k - T_{k-1} - T_{k+1}) - \bar{q}_k(2f'_k - f'_{k-1} - f'_{k+1}). \quad (4.3)$$

Denoting

$$\alpha_2(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}) \quad (4.4)$$

of Equation (4.1) by $\phi A'$.

Equations (4.3) and (4.4) can be used to evaluate $\log_e a'_k$ given by Equation (4.1) as

$$\log_e a'_k = \alpha_1(\bar{R}_k - \bar{M}_k)(2T_k - T_{k-1} - T_{k+1}) - \alpha_1\bar{q}_k(2f'_k - f'_{k-1} - f'_{k+1}) + \phi A'. \quad (4.5)$$

Equation (4.5) can be inserted in Equation (2.8) to have another expression for $\bar{q}_k$ as follows:

$$\bar{q}_k(f'_{k-1} - f'_k) = \phi A' + \alpha_1(\bar{R}_k - \bar{M}_k)(2T_k - T_{k-1} - T_{k+1}) - \alpha_1\bar{q}_k(2f'_k - f'_{k-1} - f'_{k+1}) + (\bar{R}_k - \bar{M}_k)(T_{k-1} - T_k) - \log_e(C/f)'_k$$

or

$$\bar{q}_k(f'_{k-1} - f'_k + 2\alpha_1 f'_k - \alpha_1 f'_{k-1} - \alpha_1 f'_{k+1}) = \phi A' + [\bar{R}_k - \bar{M}_k][T_k(2\alpha_1 - 1) + T_{k-1}(1 - \alpha_1) - \alpha_1 T_{k+1}] - \log_e(C/f)'_k$$

or

$$\bar{q}_k = \frac{\phi A' + [\bar{R}_k - \bar{M}_k][T_k(2\alpha_1 - 1) + T_{k-1}(1 - \alpha_1) - \alpha_1 T_{k+1}] - \log_e(C/f)'_k}{f'_k(2\alpha_1 - 1) + f'_{k-1}(1 - \alpha_1) - \alpha_1 f'_{k+1}}. \quad (5.1)$$

According to Equation (3.3) we find that 0.5 is a very good estimate for α_1 which can be inserted in Equation (5.1) to obtain

$$\bar{q}_k = \frac{\phi A' + 0.5(\bar{R}_k - \bar{M}_k)(T_{k-1} - T_{k+1}) - \log_e(C/f)'_k}{0.5(f'_{k-1} - f'_{k+1})}. \quad (5.2)$$

If sampling surveys are carried out during equal time intervals, i.e., $T_{k-1} = T_k = T_{k+1}$; Equation (5.2) becomes

$$\bar{q}_k = \frac{\phi A' - \log_e(C/f)'_k}{0.5(f'_{k-1} - f'_{k+1})}. \quad (5.3)$$

Equation (3.3) shows that α_2 is estimated at 0.04 so that $\phi A'$ becomes according to Equation (4.4) as

$$\phi A' = 0.04(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}). \quad (5.4)$$

The correction term $\phi A'$ given in Equation (5.4) can be put in another form by the inspection of the term A' shown by Equation (4.2)

$$A'_k = (\bar{R}_k - \bar{M}_k)T_k - F'_k.$$

The parameters $\bar{R}_k$ and $\bar{M}_k$ are supposed to be constant during any group of sampling surveys according to assumption 9, and Equation (1.17) we have

$$\bar{R}_k - \bar{M}_k = \bar{B}_k \quad \text{a constant}$$

$$\therefore \quad A'_k = \bar{B}_k T_k - F'_k \quad (5.5)$$

and

$$A'^2_k = \bar{B}_k{}^2 T_k{}^2 - 2\bar{B}_k T_k F'_k + F'^2_k \quad (5.6)$$

and $\phi A'$ of Equation (5.4) becomes

$$\phi A' = 0.04(\bar{R}_k - \bar{M}_k)^2(2T_k{}^2 - T_k{}^2_{-1} - T_k{}^2_{+1}) - 0.08(\bar{R}_k - \bar{M}_k)(2F'_k T_k - F'_{k-1}T_{k-1} - F'_{k+1}T_{k+1}) + 0.04(2F'^2_k - F'^2_{k-1} - F'^2_{k+1}). \quad (5.7)$$

If $T_k = T_{k-1} = T_{k+1}$ and according to Equation (1.18) we have

$$\bar{M}_k T_k = \bar{M}'_k \text{ and } \bar{R}_k T_k = \bar{R}'_k$$

$$\therefore \phi A' = -0.08(\bar{R}'_k - \bar{M}'_k)(2F'_k - F'_{k+1} - F'_{k+1}) + 0.04(2F'^2_k - F'^2_{k-1} - F'^2_{k+1}). \quad (5.8)$$

If Equation (3.2) is used to evaluate a_k,

$$a'_k \approx \frac{(\exp(\alpha_1 A'_k + \alpha_2 A'^2_k + \alpha_3 A'^3_k))^2}{\exp(\alpha_1 A'_{k-1} + \alpha_2 A'^2_{k-1} + \alpha_3 A'^3_{k-1}) \cdot \exp(\alpha_1 A'_{k+1} + \alpha_2 A'^2_{k+1} + \alpha_3 A'^3_{k+1})}$$

and

$$\log_e a'_k \approx \alpha_1(2A'_k - A'_{k-1} - A'_{k+1}) + \alpha_2(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}) + \alpha_3(2A'^3_k - A'^3_{k-1} - A'^3_{k+1}).$$

Following Equations (4.1) to (5.1) steps, we get an expression for $\bar{q}_k$ similar to Equation (5.1) with $\phi A'$ as

$$\phi A' = \alpha_2(2A'^2_k - A'^2_{k-1} - A'^2_{k+1}) + \alpha_3(2A'^3_k - A'^3_{k-1} - A'^3_{k+1}). \quad (5.9)$$

ESTIMATION OF CATCHABILITY

Denoting all terms of the numerators of Equations (5.1), (5.2), and (5.3) with the exception of $\log_e(C/f)'_k$ by "p" and their denominator by ϕF; the equations become

$$\bar{q}_k = \frac{-\log_e(C/f)'_k + p}{\phi f}. \quad (6.1)$$

Equating p to zero, a first estimate for $\bar{q}_k$ is obtained which is used together with catch data to estimate A', $\bar{R}_k$, $\bar{M}_k$, and $\phi A'$ so that p can be estimated and used to obtain the required estimate for $\bar{q}_k$ as well as other parameters.

If p has a negative sign, this means that the first estimate for $\bar{q}_k$ was higher than the true value and $p/\phi f$ is the correction to be subtracted to obtain the improved estimate and the reverse holds good as will be shown by the solved example. Equation (6.1) is therefore betterly transformed to

$$\bar{q}_k = \frac{-\log_e(C/f)'_k}{\phi f} + \frac{p}{|\phi f|}. \quad (6.2)$$

Solved examples showed that one single correction is sufficient to obtain precise estimates for $\bar{q}_k$ for populations with increasing or decreasing abundance which is a great advantage.

If a number of equations like (6.2) are available, they may be combined in a single expression as

$$\bar{q}_k = -\frac{\Sigma \log_e(C/f)'_k}{\Sigma \phi f} + \frac{\Sigma p}{\Sigma |\phi f|}. \quad (6.3)$$

EXAMPLE

Detailed informations are required to use the equations given above for estimating correctly the catchability as dividing sampling surveys into groups coinciding with seasons having more or less constant population parameters like periods with high, low, or nil recruitment, migration, natural mortality, and catchability.

As published data reviewed by the author lacked such information, it was decided to treat the hypothetical example given by Rafail (1974) so as to demonstrate the advantage of the above modified equations. Table 2 shows a part of 1974 example containing periods I and III with increasing and decreasing abundance, respectively.

Computations for Period I

A) Surveys 1, 2, and 3

$$\log_e(C/f)'_k = \log_e(1.00118) = 0.00116$$
$$\phi f = 0.5(1{,}000\text{–}2{,}000) = -500$$
$$\bar{q}_k = -0.00116/-500 = 2.320 \times 10^{-6}.$$

Above $\bar{q}_k$-estimate is used to evaluate A', $(\bar{R}'_k - \bar{M}_k)$, and $\phi A'$ using the relations:

$$F'_k = \bar{q}_k f'_k,\ N_{k0} = \text{catch}/F'_k$$
$$\exp(A'_k) = N_{k+1}/N_k$$
$$\bar{R}'_k - \bar{M}'_k = A'_k + F'_k$$
$$\hat{A}' = \bar{R}'_k - \bar{M}'^{xx}_k - F'_k.$$

TABLE 2.—A hypothetical example showing sampling periods I and III with increasing and decreasing abundance.

Period and survey k	Initial abundance N_{k0}	Effort f_k	Total mortality	Abundance coefficient A'_k	$\exp(A'_k)$	a_k	Catch $N_{k0}F'_k a_k$
Period I		$\bar{q}_k = 2 \times 10^{-6}$	$\bar{M}'_k = 0.001$	$\bar{R}'_k = 0.450$			
1	1,000,000	1,000	0.003	0.447	1.5636	1.26085	2,522
2	1,563,600	3,000	0.007	0.443	1.5575	1.25847	11,807
3	2,435,307	2,000	0.005	0.445	1.5605	1.25955	12,269
4	3,800,297	4,000	0.009	0.441	1.5543	1.25692	38,212
Period III		$\bar{q}_k = 2 \times 10^{-6}$	$\bar{M}'_k = 0.020$	$\bar{R}'_k = 0.002$			
1	5,894,992	40,000	0.100	−0.098	0.90666	0.95245	449,175
2	5,344,753	20,000	0.060	−0.058	0.94365	0.97155	207,708
3	5,043,576	10,000	0.040	−0.038	0.96271	0.98132	98,985

where $\bar{R}'_k - \bar{M}'^{xx}_k$ is the mean of available values.

All the above relations are correct except the relation $N_{k0} = \text{catch}/F'_k$ which is an approximation of $N_{k0} = \text{catch}/F'_k \cdot a_k$. If the computations show that the calculated $(\bar{R} - \bar{M})$-values are close to each other, then the approximate expression for N_{k0} is satisfactory to obtain accurate estimates for $\bar{q}_k$. Significantly different $(R - M)$-values may also lead to accurate estimates for $\bar{q}_k$. However, it may be necessary to use $\hat{A}'_k$ to estimate a_k to obtain improved estimates for N_{k0}-values to arrive at a better estimate for A'_k and $(\bar{R} - \bar{M})$-values. The rest of the computations for period I are:

K	F'_k	$N_{k0} = C/F'$	$\exp(A'_k)$	A'_k	$\bar{R}'_k - \bar{M}'_k$	$\hat{A}'_k$
1	2.32×10^{-3}	1,087,070	1.56503	0.44789	0.45021	0.44818
2	6.96×10^{-3}	1,696,408	1.55869	0.44378	0.45072	0.44354
3	4.64×10^{-3}	2,644,181			0.4505^{xx}	0.44586

According to Equation (5.4) we get

$$\hat{A}'^2_2 = 0.1967277, \hat{A}'^2_1 = 0.2008653,$$
$$\hat{A}'^2_3 = 0.1987911$$
$$\phi A' = 0.04(0.393455 - 0.399656)$$
$$= 0.04(-0.0062) = -0.000248$$
$$\phi A'/|\phi f| = -0.000248/500 = -0.496 \times 10^{-6}$$
$$\therefore \quad \bar{q}_k = (2.320 - 0.496)10^{-6} = 1.824 \times 10^{-6}.$$

According to Equation (5.8) we can calculate $\phi A'$ by another way as

$$\phi A' = -0.08(0.4505)(13.92 - 2.32 - 4.64)(10^{-3})$$
$$+0.04(96.88 - 5.38 - 21.53)(10^{-6})$$
$$= (-0.2508 + 0.0028)(10^{-3}) = -0.248(10^{-3}).$$

That is, the two methods gave the same results.

B) Surveys 2, 3, and 4

$$\log_e(C/f)'_k = 0.0009$$
$$\phi f = -500$$
$$\bar{q}_k = -0.0009/-500 = 1.8 \times 10^{-6}.$$

The following estimates are obtained by above steps

$$\bar{R}'_k - \bar{M}'^{xx}_k = 0.44782$$
$$\hat{A}'_2 = 0.44242, \hat{A}'_3 = 0.44422,$$
$$\hat{A}'_4 = 0.44062$$
$$\therefore \quad \phi A' = 0.04(0.3946628 - 0.3898815)$$
$$= 0.000191$$
$$\therefore \quad \phi A'/|\phi f| = 0.000191/500 = 0.382 \times 10^{-6}$$
$$\therefore \quad \bar{q}_k = (1.8 + 0.382)10^{-6}$$
$$= 2.182 \times 10^{-6}.$$

The arithmetic mean for $\bar{q}_k$ from the four surveys is

$$(1.824 + 2.182)(10^{-6})/2 = 4.006 \times 10^{-6}/2$$
$$= 2.003 \times 10^{-6}.$$

Equation (6.3) can be used to estimate $\bar{q}_k$ in one step as

$$\bar{q}_k = \frac{-0.00116 + 0.00090}{-1{,}000} + \frac{-0.000248 + 0.000191}{1{,}000}$$
$$= \frac{0.002060}{1{,}000} - \frac{0.000057}{1{,}000} = \frac{0.002003}{1{,}000}$$
$$= 2.003 \times 10^{-6}.$$

Period I has four sampling surveys and only two estimates for q can be obtained as the data of only three successive surveys are used to get a single q-estimate as explained above.

Computations for Period III

$$\log_e(C/f)'_k = -0.03012$$
$$\phi f = \tfrac{1}{2}(40{,}000 - 10{,}000) = 15{,}000$$
$$q_k = \frac{-0.03012}{15{,}000} = 2.008 \times 10^{-6}.$$

The following computations are obtained according to the last estimate of catchability

K	$N_{k0} = C/F_k$	$(\bar{R}'_k - \bar{M}'_k)_1$	$\hat{A}'_1$	a_k	$N'_{k0} = C/F'_k a_k$
1	5,592,318	0.00214	−0.08322	0.9595	5,828,366
2	5,172,012	−0.00788	−0.04306	0.9786	5,285,113
3	4,929,531	-0.00290^{xx}	−0.02298	0.9887	4,985,871

$(\bar{R}'_k - \bar{M}'_k)_2$	$\hat{A}'_2$
−0.01763	−0.09819
−0.01811	−0.05803
-0.01787^{xx}	−0.03795

Above estimates show a recognizable variability for the first estimated $(\bar{R}'_k - \bar{M}'_k)_1$ parameters; so the calculations are proceeded to obtain the next $(\bar{R}'_k - \bar{M}'_k)_2$-estimates which are in fact highly accurate if compared with the original values in Table 2.

Using the so-called the less accurate $\hat{A}'_1$-estimates to calculate $\phi A'$; we get

$$\phi A' = 0.04(0.0037080 - 0.0074535)$$
$$= -0.00015$$
$$\phi A'/|\phi f| = -0.00015/15{,}000 = -0.00001/1{,}000$$
$$= -0.01 \times 10^{-6}$$
$$\bar{q}_k = (2.008 - 0.010)10^{-6} = 1.998 \times 10^{-6}.$$

Using the more accurate $\hat{A}_2'$-estimates we get

$$\phi A' = 0.04(0.00673496 - 0.01108147)$$
$$= -0.000174$$
$$\phi A'/|\phi f| = -0.000174/15{,}000 = -0.011 \times 10^{-6}$$
$$\therefore \quad \bar{q}_k = (2.008 - 0.011)10^{-6} = 1.997 \times 10^{-6}.$$

Using Equation (5.8) and the more accurate $(\bar{R}_k' - \bar{M}_k')$-estimates, we get a similar result as

$$\phi A' = -0.08(-0.01787)(-0.02008)$$
$$+ 0.04(-0.0036289)$$
$$= -0.0000287 - 0.0001451 = -0.000174.$$

The above example shows that the so-called less accurate estimates gave equivalent results to the more accurate estimates. However, in situations with variable $(\bar{R}_k' - \bar{M}_k')$-values it will be preferable to compare their results with those to be obtained with the more accurate values.

DISCUSSION

Rafail (1974) showed the great advantages of his method for the estimation of some important parameters of fish populations like catchability, fishing mortality, natural mortality, and recruitment from catch data. He also showed that a similar analysis of data of tagged fish can allow the estimation of other important parameters like migrations and at the same time may correct the estimates of parameters of untagged fish that may be biased by unexpected recruitments and migrations.

The modifications presented here for expressions used to estimate catchability cause a great simplification, shortening of calculations and more accurate results. Rafail (1974) gave in his table 4 a summary of results of HP-20 computer programme for iteration of period I with increasing abundance. The results of the computer showed that after 16 iterations with a precision at six decimals and 22 iterations with a precision at nine decimals; q was estimated at 1.92×10^{-6} and 1.83×10^{-6}, respectively. The corresponding estimate by the present modified expressions was 1.824×10^{-6} by a single step. This simplification allowed the estimation of q from the next series of sampling surveys of period I (2, 3, and 4) so that an overall estimate of 2.003×10^{-6} becomes available which is highly accurate as the original value is 2×10^{-6}.

As far as period III with decreasing abundance is concerned, we find that 1974-expressions gave after three iterations 1.98×10^{-6} while the new expressions gave after one step 1.998×10^{-6} or 1.997×10^{-6} for q compared with an original value of 2×10^{-6}.

It is, therefore, concluded that the present modified expressions allow better accuracy and large economy in calculations and time during estimating q as compared with 1974-expressions. This greater accuracy of q will allow better estimates for other parameters. It appears what is a logic conclusion that the larger number of surveys, the larger will be the number of available q-estimates allowing a more accurate evaluation for catchability and other parameters.

SUMMARY

Modifications are presented here for expressions given by Rafail (1974) for estimating catchability to evaluate fishing and natural mortalities, recruitment, and migration assuming seasonal and subpopulation variability and the constancy of the parameters within the seasons. These modifications depend on the relation

$$(\exp(A_k') - 1)/A_k' = \exp(\pm 0.5A_k' + 0.04A_k'^2)$$

where A_k' denotes the instantaneous rate of change of fish abundance during the kth sampling period. The above expression is an extension of Paloheimo (1961) expression and gave a maximum error less than 1% when A' lies between ± 3.0 and smaller errors at smaller values of A so that the errors are less than 0.2% when A' lies between ± 2.5. This expression can be considered as highly accurate in the range that is always encountered in fisheries studies.

The modified expressions allow a large economy in calculations and time and a better accuracy for the estimation of catchability.

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IDENTIFICATION OF FISH SPECIES BY THIN-LAYER POLYACRYLAMIDE GEL ISOELECTRIC FOCUSING

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ABSTRACT

Conventional electrophoretic techniques for the identification of fish species are limited in the resolution and reproducibility needed for the reliable identification of fish species. This paper describes the potential of a high resolution protein separation technique, thin-layer polyacrylamide gel isoelectric focusing (IEF), as a new means of identifying fish species. Sarcoplasmic protein patterns are shown for 11 species of commercially important New England fishes under both low resolution (pH 3.5–10 gradient) and high resolution (pH 3.5–5 gradient) conditions. The reproducibility of the protein patterns and pH gradients from day to day is also shown. The inherent high resolution and excellent reproducibility of IEF should allow the positive identification of fish species without the costly procedure of maintaining a supply of known species for use as standards.

Many different electrophoretic techniques have been used for the identification of fish species. Protein extracts from several species of fishes were first compared using moving boundary electrophoresis (Connell 1953). Differences in the electrophoretic protein patterns between species formed a "fingerprint" for each. In an effort to obtain higher resolution and reproducibility of the protein patterns, starch gel zone electrophoresis was applied as a method for diffentiating fish species (Thomson 1960). Subsequent attempts to further improve species identification techniques centered on the investigation of new stabilizing media. The use of polyacrylamide gels (Payne 1963; Cowie 1968) and agar gels (Hill et al. 1966) resulted in shortened analysis times, increased resolution, and easier handling and storage of gels. A rapid identification technique based on cellulose acetate electrophoresis (Lane et al. 1966) has found widespread use in quality control.

Each of these electrophoretic techniques (except moving boundary electrophoresis) is still in common use and has contributed much towards eliminating problems of species substitution. Unfortunately, each of these techniques is subject to one or more limitations that lessen its effectiveness as a routine species identification test. Variations in stabilizing media composition, sample application technique, separation time, applied voltage or current, and the technician's skill indicated the need for simultaneously running known species along with unknown samples to obtain a reliable identification. Collaborative studies of the two most widely used species identification procedures, disc electrophoresis (Thomson 1967) and cellulose acetate electrophoresis (Learson 1969, 1970), showed that reproducibility of specific protein patterns from analysis to analysis was a major problem.

This paper describes the potential of a high resolution protein separation technique, thin-layer polyacrylamide gel isoelectric focusing (IEF), as a new means of identifying fish species. IEF is an equilibrium technique in which proteins are separated according to their isoelectric points in a reproducible natural pH gradient. The pH gradient is formed in the gel by the electrolysis of amphoteric buffer substances called carrier ampholytes. Protein molecules migrate in the electric field along the pH gradient until they reach the pH equal to their isoelectric point. Here the protein has a net charge of zero, and no further migration can take place. The proteins become concentrated into very sharp bands and molecules whose isoelectric points differ by 0.07 pH units (pH 3.5–10 gradient) or 0.02 pH units (pH 3.5–5 gradient) may be resolved.

PROCEDURE

Isolation of Sarcoplasmic Proteins

Fresh iced fish was obtained from various Glou-

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cester fish processors. Four specimens of each species were examined except for cod and haddock where 15 individuals each were examined. All fish were held on ice from purchase to filleting. Fillets were held at 8°C until extraction of sarcoplasmic proteins.

Sarcoplasmic protein extracts were prepared by blending 100 g of muscle tissue with 200 ml of distilled water in a 500-ml Waring[2] blender jar. A Teflon baffle shaped to fit the inside contour of the blender jar about 1 cm below the water level was used to prevent the incorporation of air bubbles during the blending operation. The distilled water, blender jar, and baffle were chilled to 8°C prior to use to prevent protein denaturation from heat generated during blending. The resulting mixture was centrifuged at 1,400 *g* for 30 min at 4°C in an International PR-2 Refrigerated Centrifuge. The resulting supernatant was used for analysis without any further purification.

Preparation of Polyacrylamide Gel Slab

The polyacrylamide gel slab was chemically polymerized between a glass plate and an acrylic template. The glass plate and acrylic template were separated by a 0.75-mm acrylic spacer that extended around three sides leaving the top open. The template had embedded teeth that formed sample wells in the gel surface. The gel slabs used in these experiments were 175 mm × 90 mm × 0.75 mm and contained 12 sample wells, each capable of holding up to 5 μl.

A 4% (wt/vol) polyacrylamide gel containing 2% (wt/vol) carrier ampholytes was prepared as follows:

Into a 25-ml Erlenmeyer flask was pipetted
- 8.2 ml distilled water
- 3.0 ml 50% (vol/vol) glycerol (final concentration 10% [vol/vol])
- 3.0 ml 20% (wt/vol) acrylamide (final concentration 4% [wt/vol]) plus 0.8% (wt/vol) bisacrylamide (final concentration 0.16% [wt/vol])
- 5.0 μl tetramethylethylenediamine (final concentration 0.03% [wt/vol])
- 0.75 ml 40% (wt/vol) ampholine of appropriate pH range (final concentration 2% [wt/vol]).

This solution was degassed under vacuum for 4 min. Polymerization was started with the addition of 50 μl 10% (wt/vol) ammonium persulfate (final concentration 0.03% [wt/vol]). After a final degassing under vacuum for one more minute, the solution was immediately pipetted into the gel mold. The top of the gel solution was layered with water to form an even surface. Polymerization was complete in 20 min at room temperature. The open top of the gel mold was then sealed with masking tape, and the whole assembly was placed in a refrigerator (8°C) overnight before use. A supply of gel slabs may be prepared and stored for 2 wk in this manner. After the gel had polymerized, the template and spacer were removed leaving the gel adhering to the glass plate.

Electrofocusing Procedure

Electrofocusing was carried out using a Medical Research Apparatus Slab Electrofocusing Apparatus, Model M-150. The gel slab was placed on the cooling platform and cooled to −2°C prior to sample application. To insure good thermal contact, a layer of light paraffin oil was used between the glass plate and the cooling platform. After the gel slab had cooled, 5 μl of the protein extract was pipetted into a sample well with a micropipette. Up to 12 samples may be compared in a single gel slab. Felt strips soaked in 1M NaOH (catholyte) and 1M H_3PO_4 (anolyte) were applied to the edges of the gel to provide electrical contact with the platinum wire electrodes. A power supply was connected to the electrodes, and power was applied until equilibrium focusing was attained. Both constant-power and constant-voltage power supplies were used in these experiments. In isoelectric focusing, a power supply capable of delivering constant power is preferred. Using a constant power of 10 W, equilibrium focusing was complete in 1.5–2.0 h. Using constant voltage, the voltage must be manually increased to compensate for increased resistance through the gel as the pH gradient forms. Separation times are longer (5–6 h) and resolution suffers due to joule heating within the gel. With either type of power supply, equilibrium focusing is attained and the reproducibility of the protein patterns is not affected. After electrofocusing is complete, the pH gradient may be measured as a check on reproducibility or to determine the isoelectric points of the separated proteins. The plate is warmed to room temperature and the pH gradient

[2]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

is measured using a 3-mm diameter Ingold microcombination surface pH electrode and Corning Model 101 digital pH meter. The electrode was calibrated with standard pH buffer solutions at room temperature.

The protein patterns were stained with Coomassie Blue R-250 and destained in 10% ethanol–10% acetic acid (Righetti and Drysdale 1974). After destaining, the gels may be air dried and stored indefinitely.

RESULTS AND DISCUSSION

Figure 1 shows typical protein patterns for 11 species of commercially important New England fishes. The pH gradient in this gel runs from pH 3.5 at the top (anode) to pH 10.0 at the bottom (cathode). The pattern for each species appeared to be unique and demonstrated resolution not normally attained by conventional electrophoretic techniques. Closely related species such as cod and haddock or red hake and white hake show similarities in overall patterns, but enough differences are present to permit a positive identification.

Due to the large number of protein bands resolved in the pH 3.5–10.0 gradient, many of which have the same isoelectric point, it is sometimes advantageous to look at only a small portion of the pattern under increased resolution. Figure 2 shows the same 11 species compared in a pH 3.5–5.0 gradient. The resolution is much greater and identification is not complicated by the presence of as many proteins with the same isoelectric point from species to species.

Figures 3 and 4 illustrate the reproducibility of the protein patterns through a time interval. The proteins in Figure 3 were focused in 2.5 h using a constant power of 10W. The proteins in Figure 4 were focused in 5.5 h using a constant-voltage power supply. The voltage was manually increased from 100 V to 300 V in hourly 100-V intervals. The voltage was then held constant at 300 V for 3.5 h. The proteins in both plates have been focused to equilibrium, and the pattern for each species is reproducible.

The protein patterns one obtains in isoelectric focusing are dependent on the pH gradient formed in the gel. Commercially prepared carrier ampholytes form pH gradients that remain stable and reproducible during the time necessary for the complete equilibrium focusing of sarcoplasmic proteins. Figure 5 shows the pH gradients formed in the previous two figures. The pH gradient curve labeled "A" corresponds to the plate in Figure 3, and the one labeled "B" corresponds to the plate in Figure 4. The slightly lower position of pH gradient A is also seen by the displacement of the patterns in Figure 3 toward the lower end of the gel (cathode). This slight shift of the pH gradient, however, was not enough to affect the reproducibility of the protein patterns.

Isoelectric focusing offers several advantages over electrophoretic techniques for the identification of fish species. Isoelectric focusing is an equilibrium technique where the proteins are limited in how far they can travel by the pH gradient. Since proteins have a net charge of zero at their isoelectric point, no migration beyond that point can take place. Diffusion of the isoelectric proteins is prevented by the electric field. During the course of a normal electrofocusing experiment, as long as the pH gradient remains stable, the protein patterns will not vary. In contrast, protein patterns from conventional electrophoretic techniques are time dependent and may suffer loss of resolution due to diffusion.

Another advantage of isoelectric focusing over conventional electrophoretic techniques is the ease of sample application. Samples were applied directly from micropipettes into molded sample wells. Samples may also be applied as a drop or streak on the gel surface or by placing a small rectangle of filter paper saturated with the sample directly on the gel. The position of sample application may be at any point on the gel slab. While some of these sample application techniques may be common to other electrophoretic procedures, only in IEF may these techniques be used interchangeably without affecting the protein patterns. This versatility is an important asset. Dilute extracts (e.g., when the amount of muscle tissue available is unavoidably small) may be applied in a large volume to obtain a protein pattern comparable to that obtained with a small volume of a concentrated extract (e.g., a drip fluid sample from a recently frozen fish). Large sample volumes may also be applied so that minor components may be detected and compared between species. The ability to vary the position of sample application without affecting the protein pattern eliminates one more possibility for human error. Sample application technique in conventional electrophoretic methods affects the protein pattern. Samples must be carefully applied as a thin

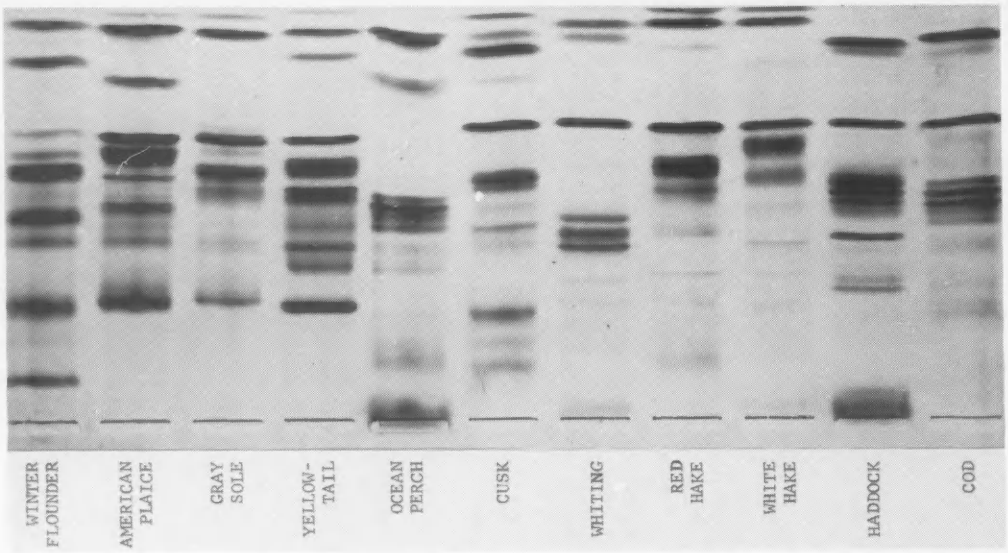

FIGURE 1.—Sarcoplasmic protein patterns from 11 species of fishes focused in a pH 3.5–10 gradient. The species are from left to right: winter flounder, *Pseudopleuronectes americanus*; American plaice, *Hippoglossoides platessoides*; gray sole, *Glyptocephalus cynoglossus*; yellowtail, *Limanda ferruginea*; ocean perch, *Sebastes marinus*; cusk, *Brosme brosme*; whiting, *Merluccius bilinearis*; red hake, *Urophycis chuss*; white hake, *Urophycis tenuis*; haddock, *Melanogrammus aeglefinus*; and cod, *Gadus morhua*.

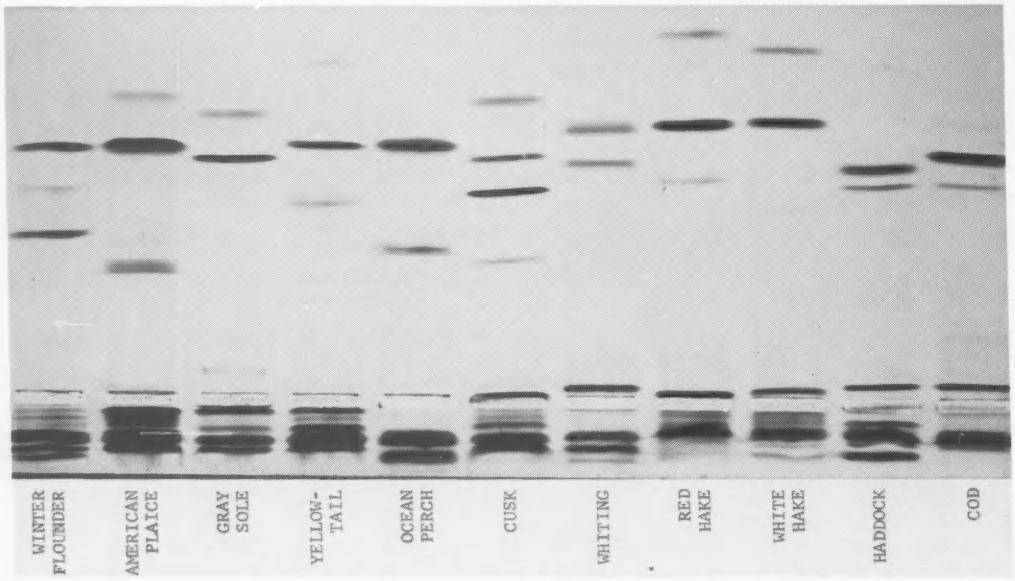

FIGURE 2.—Sarcoplasmic protein patterns from 11 species of fishes focused in a pH 3.5–5 gradient. The species arrangement is the same as shown in Figure 1. Note that the bands separated in Figure 2 correspond to the bands shown in the upper portion of the gel in Figure 1.

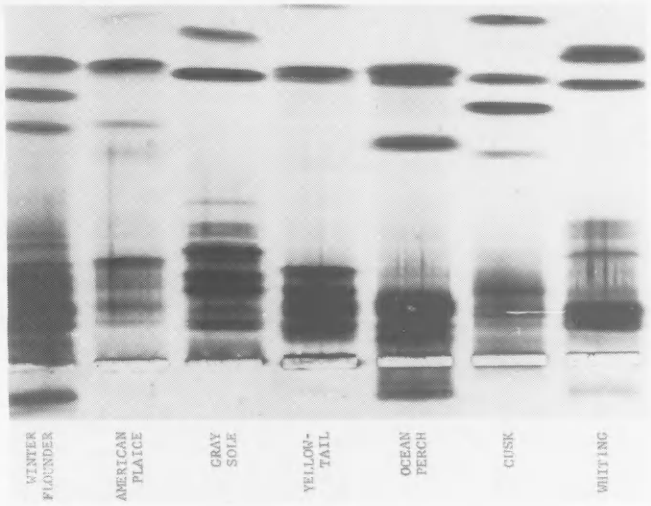

FIGURE 3.—Sarcoplasmic protein patterns from seven species of fishes focused in a pH 3.5–5 gradient under constant power conditions. The species are from left to right: winter flounder, *Pseudopleuronectes americanus*; American plaice, *Hippoglossoides platessoides*; gray sole, *Glyptocephalus cynoglossus*; yellowtail, *Limanda ferruginea*; ocean perch, *Sebastes marinus*; cusk, *Brosme brosme*; and whiting, *Merluccius bilinearis*.

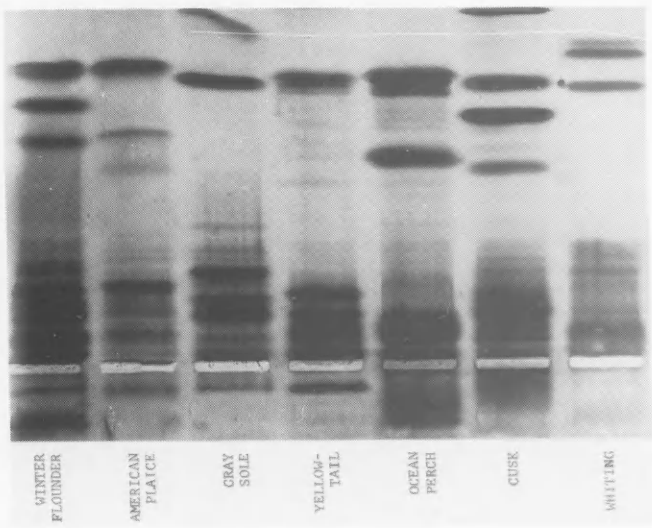

FIGURE 4.—Sacroplasmic protein patterns from seven species of fishes focused in a pH 3.5–5 gradient under constant voltage conditions. The species arrangement is the same as shown in Figure 3. Figures 3 and 4 illustrate the reproducibility of the protein patterns for seven species of fishes on two successive days.

zone at a particular position to obtain a satisfactory separation. Isoelectric focusing is actually less demanding in experimental technique when compared to electrophoresis, yet still offers increased resolution and reproducibility.

Due to the limited number of individuals and species studied, additional work is underway to increase the reliability and potential of IEF as a species identification test. Additional species will be compared. Their protein patterns will be added to a library of standard IEF protein patterns. Additional individuals from each species will be tested for variations in protein patterns due to size, sex, season, or geographical origin. Variations in some minor components of the protein patterns for some species after frozen storage have been observed. Work is planned to examine this in greater detail. The use of commercially prepared polyacrylamide gel slabs will reduce variations in stabilizing media composition and eliminate gel preparation time. These ready prepared gels used with a high-voltage constant-power

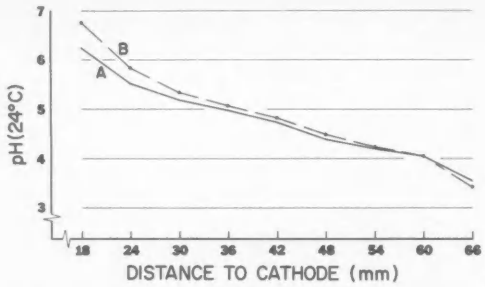

FIGURE 5.—Reproducibility of pH gradients. Measurements of pH were taken after focusing the gels shown in Figures 3 and 4. The pH gradient A corresponds to the pH measurements taken from the gel in Figure 3. The pH gradient B corresponds to the pH measurements taken from the gel in Figure 4. (The pH gradients do not match exactly because the platinum electrodes were not placed with the same relative sample well to cathode distance. The only effect this has on the protein patterns is to shift them either up or down. Relative distances between the various proteins in the pattern remain essentially the same.) The similarity of these two pH gradients may be correlated with the reproducibility of the protein banding patterns shown in Figures 3 and 4.

power supply should produce high quality sarcoplasmic protein patterns in 1.0–1.5 h. New protein staining methods have been investigated that allow staining of the protein patterns in 15–30 min with no destaining required. Using these improvements, samples may be identified in less than 2 h.

CONCLUSIONS

Thin-layer polyacrylamide gel isoelectric focusing has been shown to be a promising technique for the identification of fish species. The inherent high resolution of this method allows the production of characteristic protein patterns of a quality not normally attained by conventional electrophoretic techniques. The excellent reproducibility of this technique should allow the positive identification of fish species without maintaining a supply of known species for use as standards. Investigations utilizing commercially prepared gel slabs, high-voltage constant-power power supplies, and rapid staining techniques promise to produce an extremely reliable procedure for the routine identification of fish species.

ACKNOWLEDGMENT

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VARIOUS SPECIES OF PHYTOPLANKTON AS FOOD FOR LARVAL NORTHERN ANCHOVY, *ENGRAULIS MORDAX*, AND RELATIVE NUTRITIONAL VALUE OF THE DINOFLAGELLATES *GYMNODINIUM SPLENDENS* AND *GONYAULAX POLYEDRA*

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ABSTRACT

First feeding northern anchovy larvae were presented with a variety of phytoplankters common to coastal waters of southern California to determine which species are acceptable as food. Most of the larvae ate the four species of dinoflagellates tested in feeding experiments but did not feed on diatoms or small flagellates. Larval rearing experiments were conducted to compare the nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra*, two species of dinoflagellates readily eaten by anchovy larvae and known to predominate in the chlorphyll maximum layers off the southern California coast. *Gymnodinium splendens* was a nutritional food for the first 10 days of larval life, but *Gonyaulax polyedra* was judged to be inadequate. Supplementing the *G. polyedra* diet with microzooplankton increased larval survival comparable to survival on a microzooplankton diet alone. When the *Gymnodinium splendens* diet was supplemented with microzooplankton, the larvae grew faster but survival did not increase. Results are discussed in relation to studies on larval survival in the Southern California Bight during 1974 and 1975.

The strength of a year class of fish may depend on availability of food organisms during the early larval stages (May 1974). Consequently, there have been attempts to assess the abundance of planktonic organisms in larval feeding areas as a step towards predicting year class success (Shelbourne 1957; Bainbridge and Forsyth 1971; Lasker 1975, in press). For this approach to be successful, additional information is also necessary concerning: 1) selection of prey by the fish larvae, 2) concentration and size of food organisms necessary to initiate feeding by the fish larvae, 3) nutritional value of the food that the larvae select, and 4) temporal and spatial distribution of the food organisms in the feeding area.

The northern anchovy, *Engraulis mordax*, larva has been studied in the laboratory and many criteria for successful feeding have been determined (Lasker et al. 1970; O'Connell and Raymond 1970; Hunter 1972, 1976; Hunter and Thomas 1974). Results of these studies indicate that first feeding anchovy larvae require small particles (<100 μm in smallest dimension) at relatively high densities to initiate feeding and to insure moderate survival. O'Connell and Raymond (1970) found in laboratory experiments that anchovy larvae reared in seawater containing 1 copepod nauplius/ml or less experienced heavy mortalities during the sixth and seventh days after hatching. To date such a high concentration has not been found in the nearshore region of the California Current (Beers and Stewart 1967, 1969). However, the possibility does exist that anchovy larvae could survive on some of the larger phytoplankters during early stages of development (Hunter and Thomas 1974). Lasker et al. (1970) found that anchovy larvae would feed and grow to a length of 5 to 6 mm in the laboratory on a diet of the naked dinoflagellate, *Gymnodinium splendens*. With this in mind, Lasker (1975) used laboratory-spawned anchovy larvae to test for feeding activity in seawater pumped from the surface and chlorophyll maximum layer in the nearshore region of the Southern California Bight. Lasker found that during March and April 1974 there were sufficient numbers of *G. splendens* (>20 organisms/ml) in the chlorophyll maximum layer for initiation of feeding by anchovy larvae. During 1974 and 1975, Lasker (in press) monitored the plankton distribution off the southern California coast in an effort to establish a

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relationship between oceanographic conditions and larval anchovy food organisms. In 1975 he found that *G. splendens* was replaced as the dominant organism in the chlorophyll maximum layer by the armored dinoflagellate, *Gonyaulax polyedra*, and later by a variety of small diatoms. In an effort to assess effects that this succession might have on survival of anchovy larvae, we have conducted feeding experiments with some of the phytoplankters common in the Southern California Bight to determine which species are acceptable as food by anchovy larvae. In addition, we have examined the relative nutritional value of *Gymnodinium splendens* and *Gonyaulax polyedra*.

METHODS AND MATERIALS

Phytoplankton Cultures

The phytoplankters chosen for feeding experiments are common to southern California coastal waters, and most were major components of the chlorophyll maximum layers during 1974 and 1975 (Lasker in press). Also, they were of an appropriate size for ingestion by first feeding anchovy larvae (Table 1). Axenic cultures of the selected phytoplankters were supplied by James Jordan of the Food Chain Research Group at Scripps Institution of Oceanography. Culture techniques were described by Thomas et al. (1973).

TABLE 1.—Average dimensions of phytoplankters offered as food to first feeding anchovy larvae.

BACILLARIOPHYCEAE:	
Ditylum brightwellii (25 × 150 μm, single cells)	
Chaetoceros affinis (4 μm wide in chains to 200 μm)	
Thalassiosira decipiens (8 × 10 μm, single cells)	
Leptocylindrus danicus (5 μm wide in chains to 75 μm)	
DINOPHYCEAE:	CHLOROPHYCEAE:
Gymnodinium splendens (51 μm)	*Chlamydomonas* sp. (10 μm)
Gonyaulax polyedra (40 μm)	*Dunaliella* sp. (6 μm)
Prorocentrum micans (27 × 38 μm)	
Peridinium trochoideum (20 μm)	

Feeding Experiments

To determine which phytoplankters are preyed upon by anchovy larvae, feeding experiments were conducted using methods similar to those of Lasker (1975). Cylindrical 8-liter battery jars, wrapped with dull black cardboard, were filled with approximately 5 liters of filtered seawater (filter pore size, 5 μm) and inoculated from a dense culture of the phytoplankton to be tested. The densities were determined by counting organisms in 1-ml alilquots in a Sedgwick–Rafter[3] counting chamber and/or with a Coulter Counter Model Ta, and the size was measured with an ocular micrometer. Experiments were conducted at temperatures ranging from 16.9° to 19.6°C, and the test jars were illuminated from above with a bank of four 40-W fluorescent lamps. Light intensity at the surface of the test jars was approximately 2,400 lx. Because anchovy larvae readily feed on *Gymnodinium splendens* (Lasker 1975), at least one container in each series of experiments contained only this food organism as a control to test the feeding ability of each batch of larvae.

Diatoms were maintained in suspemsion during the feeding trials by a gentle stream of bubbled air in each test jar. To evaluate the effect of such agitation on the ability of larvae to feed, experiments were conducted with and without bubbled air using *G. splendens* as food. Little effect on feeding ability could be detected (Table 2, Trial 1).

Anchovy eggs were obtained from adult anchovies maintained in spawning condition at the Southwest Fisheries Center Laboratory. Spawning techniques were described by Leong (1971). Anchovy eggs and larvae were allowed to develop in 1-liter jars (100 eggs/jar) containing filtered seawater (filter pore size, 5 μm). First feeding larvae (2.5 days after hatching at 17°C) were placed in the experimental containers with the test organism for approximately 8 h before being siphoned from the containers and quickly immobilized on a membrane filter (pore size, 8 μm) by vacuum filtration. This technique helped to prevent the larvae from defecating (Lasker 1975). The larvae remained somewhat transparent after air drying so that the presence of food in the gut could be determined by microscopic examination of the intact animal.

Larval Rearing Experiments

Anchovy larvae were reared for 10 days in 10-liter circular containers immersed in a temperature-controlled bath in an air-conditioned room (Lasker et al. 1970). The containers were filled with membrane filtered seawater (pore size, 0.45 μm), the salinity was 33.4‰, and the temperature was maintained at 16.0° ± 1.1°C. Lighting

[3]Mention of trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 2.—Laboratory feeding experiments showing the percentage of anchovy larvae that fed on: 1) diatoms—*Ditylum brightwellii, Chaetoceros affinis, Thalassiosira decipiens,* and *Leptocylindrus danicus*; 2) dinoflagellates—*Gymnodinium splendens, Gonyaulax polyedra, Prorocentrum micans,* and *Peridinium trochoideum*; and 3) flagellates—*Chlamydomonas* sp. and *Dunaliella* sp.

Feeding trial no. (duration in hours)	Temp (°C)	Air-stone	Food organism	Concentration of food particles (organisms/ml)	Number of larvae per experiment	Feeding by anchovy larvae		
						% of larvae with ¼ to full gut	% of larvae with <⅛ particles in gut	% of larvae with empty gut
1 (7.25)	18.2		*G. splendens*	162	65	65	7	28
	18.2	X	*G. splendens*	162	54	48	9	43
	18.2	X	*G. splendens*	162	70	53	16	31
2 (8.0)	18.2		*G. splendens*	180	70	33	16	51
	18.5	X	*D. brightwellii*	164	59	0	0	100
	19.6	X	*D. brightwellii*	164	46	0	0	100
3 (8.0)	17.0		*G. splendens*	240	67	67	16	17
	17.0	X	*C. affinis*	127 chains	59	0	0	100
	17.0	X	*C. affinis*	127 chains	80	0	0	100
	17.0	X	*T. decipiens*	154	73	0	0	100
	17.0	X	*T. decipiens*	205	69	0	0	100
4 (8.0)	17.1		*G. splendens*	195	60	55	7	38
	16.9	X	*L. danicus*	197 chains	75	0	0	100
	16.9	X	*L. danicus*	780 chains	57	2	0	98
5 (8.0)	17.4		*G. splendens*	208	62	34	10	56
	17.7		*P. trochoideum*	56	65	67	22	11
	17.7		*P. trochoideum*	97	54	65	7	28
	17.7		*P. trochoideum*	210	46	50	26	24
	17.7		*Chlamydomonas* sp.	211	46	0	0	100
	17.7		*P. micans*	201	38	45	21	34
6 (8.0)	18.2		*G. splendens*	193	26	58	23	19
	18.2		*G. polyedra*	102	58	78	7	15
	18.2		*G. polyedra*	60	48	60	10	30
	17.7		*Dunaliella* sp.	303	67	0	0	100
	17.7		*Dunaliella* sp.	242	31	0	0	100

was provided for 14 h/day by 40-W fluorescent lamps as described earlier.

Eight rearing containers were inoculated with *G. splendens* and eight with *Gonyaulax polyedra* at a concentration of 100 organisms/ml. As a supplement to these food organisms, some containers were also stocked with a combination culture of the rotifer, *Brachionus plicatilis,* and the harpacticoid copepod, *Tisbe holothuriae,* with final concentrations of 0.0, 0.1, 1.0, and 5.0 organisms/ml (Table 3). Duplicate experiments were run simultaneously for all treatments including two containers without dinoflagellates but stocked with *B. plicatilis* and *T. holothuriae,* at a concentration of 5 organisms/ml.

The relative proportions of *B. plicatilis* and *T. holothuriae* (hereafter also referred to as microzooplankton) in the larval rearing containers

TABLE 3.—Survival and growth of anchovy larvae reared for 10 days on different diet regimes.

Stocking density of larvae on day 0 (no./liter)	Concentration of dinoflagellate (organisms/ml)	Concentration of microzooplankton (organisms/ml)	Survival		Standard length (mm)		Average weight (mg)
			Number	Percent	Mean	S_X	
	Gymnodinium splendens						
3.3	100	5.0	11	33.3	4.24	0.359	0.039
3.4	100	5.0	15	44.1	4.87	0.671	0.048
2.2	100	1.0	5	22.7	4.30	0.480	0.061
2.5	100	1.0	12	48.0	4.73	0.677	0.047
3.1	100	0.1	13	41.9	4.46	0.355	0.046
3.9	100	0.1	6	15.4	3.57	0.314	0.046
2.8	100	0.0	9	32.1	4.23	0.485	0.042
3.6	100	0.0	8	22.2	4.03	0.413	0.056
	Gonyaulax polyedra						
3.3	100	5.0	5	15.2	4.02	0.403	0.065
3.9	100	5.0	14	35.9	4.82	0.710	0.059
3.8	100	1.0	5	13.2	4.54	0.796	0.077
3.7	100	1.0	7	18.9	4.41	0.219	0.057
2.8	100	0.1	1	3.6	3.7	—	(1)
2.9	100	0.1	1	3.5	4.0	—	(1)
3.5	100	0.0	1	2.9	3.0	—	(1)
3.9	100	0.0	0	0.0	—	—	—
4.2	0	5.0	8	19.1	4.51	0.669	0.050
2.3	0	5.0	0	0.0	—	—	—

[1]Sample too small to weigh.

varied during the course of the experiment. Initially, approximately 90% of the microzooplankters in the containers were *T. holothuriae*, but by the end of the rearing experiment, *B. plicatilis* was the dominant organism (97%). We were unable to determine if the anchovy larvae were selectively feeding on the copepods because the combination culture of microzooplankton which was used to stock the larval rearing containers also experienced a similar succession in species dominance during the experimental period.

Brachionus plicatilis and *T. holothuriae* were cultured together in the same vessel using techniques described by Hunter (1976). The cultures were filtered through 105-μm screening to remove the largest organisms before inoculating the larval rearing containers. Microscopic examination of the filtrate revealed a predominance of small rotifers and copepod nauplii.

Fifty anchovy eggs were added to each container the day after spawning and the appropriate dinoflagellate was also introduced at this time. Hatching occurred on the next day, which corresponds to day 0 of the experiment. The number of dead embryos on the container bottom was counted at this time and the percentage hatch was calculated. On day 2, most of the yolk sac was absorbed, the eyes were pigmented, and the larvae initiated feeding. At this time, the microzooplankton were added. The experiments were terminated on day 10; standard lengths were measured for each animal; average dry weight for larvae in each container was determined; and the percent survival in each container was calculated.

Each larval rearing container was sampled daily to monitor the concentration of food organisms. Because *Gymnodinium splendens* and *Gonyaulax polyedra* tend to form patches, 1-ml samples were taken from three different locations in the tank outside of a patch; the numbers were averaged and an appropriate amount of a dense dinoflagellate culture was added daily to maintain a concentration of 100 organisms/ml. The density of *B. plicatilis* and *T. holothuriae* was maintained in a like manner except that the volume sampled was larger (from 10- to 100-ml samples/container, depending on the stock density of microzooplankton). Also, we were careful to sample a few centimeters away from the container surfaces because *T. holothuriae* copepodids and adults are thigmotactic. We stocked the rearing containers with nauplii (which are less thigmotactic than the older stages). However, during the course of the experiments, surviving *T. holothuriae* developed beyond the naupliar stages and tended to settle out on container surfaces becoming less available to anchovy larvae. These stages were not included in our counts.

RESULTS

Feeding Experiments

A total of 518 larvae were presented with four species of diatoms (Table 2). Only one larva fed on diatoms. This single individual ate a narrow (5 × 50–75 μm) chain-forming diatom, *Leptocylindrus danicus*.

Most larvae fed on the dinoflagellates *Gymnodinium splendens*, *Gonyaulax polyedra*, *Prorocentrum micans*, and *Peridinium trochoideum*. There was no apparent preference by larvae for a particular species of dinoflagellate. Between 72 and 89% of the larvae tested fed on *P. trochoideum* (20 μm), which are as small as the smallest sized particles known to be ingested by first feeding anchovy larvae (Arthur 1976). *Peridinium trochoideum* is a darkly pigmented dinoflagellate. Perhaps this characteristic makes it more visible to the larvae than other particles of a similar size. Lasker (1975) concluded that first feeding anchovy larvae required a particle greater than 40 μm to fill their gut in 8 h.

Anchovy larvae did not feed on the smallest prey used in the feeding experiments, the flagellates *Chlamydomonas* sp. (10 μm) and *Dunaliella* sp. (6 μm).

Larval Rearing Experiments

Growth and survival of anchovy larvae reared for 10 days on different diet regimes are shown in Table 3. The survival rate of larvae reared on the *Gymnodinium splendens* diet was higher than on the *Gonyaulax polyedra* diet. The relationship between larval survival and supplementation of the dinoflagellate diet with microzooplankton was described with linear regressions (Figure 1). The survival of larvae reared in seawater containing 100 *Gymnodinium splendens*/ml did not significantly increase (t for the slope of the regression = 0.1, $P<0.20$) when microzooplankton were added to their diet as a supplement (Figure 1). Supplementation of the *Gonyaulax polyedra* diet with microzooplankton did result in a significant increase (t for the slope of the regression = 3.24,

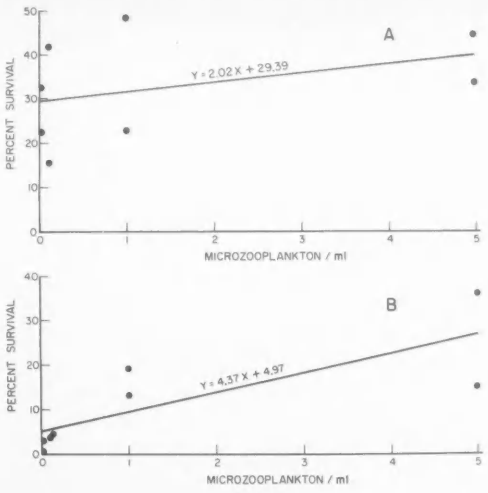

FIGURE 1.—Percent survival of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

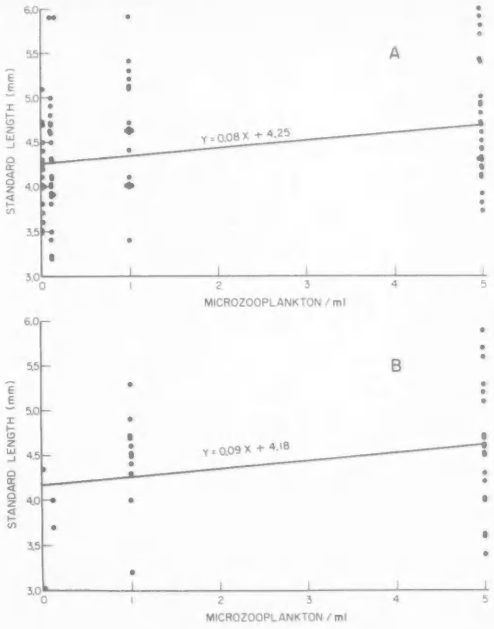

FIGURE 2.—Standard lengths of *Engraulis mordax* at 10 days in relation to supplementation of a dinoflagellate diet with microzooplankton. A) *Gymnodinium splendens* diet. B) *Gonyaulax polyedra* diet.

$P<0.025$) in larval survival. Larvae reared on a *G. polyedra* diet required at least 1 microzooplankton/ml in order to have survival rates that were comparable to larvae reared on a diet of *Gymnodinium splendens*. These results were comparable to the survival rates recorded by O'Connell and Raymond (1970) for anchovy larvae fed copepod nauplii at various concentrations. They found that larvae did not survive for 12 days in containers with less than 1 nauplius/ml.

Although anchovy larvae grow slowly during the first several days of feeding, a slight but significant increase ($t = 2.67$, $P<0.05$) in standard length occurred in larvae fed *G. splendens* when their diets were supplemented with microzooplankton (Figure 2), but no differences in dry weight were detected. Larvae fed *Gonyaulax polyedra* also appeared to increase in standard length when their diets were supplemented (Figure 2), but because the increase was slight and the number of data points was small due to the low survival rates on this diet, no significant increase was detected ($t = 1.50$, $P>0.20$).

Survival was low in larvae fed only 5 microzooplankters/ml without any dinoflagellates (Table 3). One container had no survivors and the other had 19.9% survival. Theilacker and McMaster (1971) found that larval anchovies that were fed only rotifers (*B. plicatilis*) had a lower rate of survival than those fed *Gymnodinium splendens* and *B. plicatilis* in combination. They related this finding to the low feeding success of larvae on the larger sized rotifers during the first few days of feeding. Also, Houde (1973) believes that survival of fish larvae is increased when blooms of phytoplankton are maintained in rearing containers to "condition" the water (presumably by removing metabolites).

DISCUSSION

Anchovy larvae apear to select their prey and it seems as if size is not the only criterion for selection. Larvae did not feed on any of the four species of diatoms tested in this study. The most obvious explanation is that spines and other processes on the diatoms either discouraged the larvae from striking or prevented them from swallowing. On the other hand, most larvae fed on all species of dinoflagellates tested. Visibility might also play an important role in prey selection since the darkly pigmented dinoflagellate, *P. trochoideum*,

was heavily preyed upon by anchovy larvae even though *P. trochoideum* are as small as the smallest particles detected by Arthur (1976) in the guts of larval anchovies.

It appears that prey differ in their nutritional value to anchovy larvae. *Gymnodinium splendens* and *Gonyaulax polyedra* are readily eaten by anchovy larvae, but *G. polyedra* was an inadequate food. Only 1 larva of the 74 that were reared on an exclusive diet of *G. polyedra* survived for 10 days. Larvae reared on a diet of *G. polyedra* supplemented with microzooplankton had survival rates that increased relative to the degree of supplementation. Although certain species of *Gonyaulax* are known to be toxic, it seems unlikely that this was a cause of mortality in our experiments because survival was good when larvae were fed *G. polyedra* supplemented with 5 microzooplankters/ml.

We offer two possible explanations for the difference in the nutritional value of the two dinoflagellates: 1) *G. polyedra* is about 10 μm smaller in diameter than *G. splendens*. Therefore, on the basis of volume alone, *G. splendens* could have twice as many calories as *Gonyaulax polyedra*, because the volume increases as the cube of the radius in a sphere. 2) *G. polyedra* is armored while *Gymnodinium splendens* is not, and, therefore, *G. splendens* is presumably more digestible by anchovy larvae which have an undifferentiated gut during the early stages of their development. Lasker et al. (1970) found that the armored dinoflagellate, *Prorocentrum micans* (27 $\times$ 38 μm), did not sustain life in first feeding anchovy larvae but again, this organism is smaller than *G. splendens*.

Lasker (1975) concluded that the nearshore area of the Southern California Bight was a good feeding ground for first feeding anchovy larvae during the spring of 1974 because of the high concentrations of *G. splendens* found in the chlorophyll maximum layer. In this study, the survival of anchovy larvae fed 100 *G. splendens*/ml was acceptable, and it did not differ from that of larvae fed a *G. splendens* diet supplemented with microzooplankton at concentrations up to 5 organisms/ml. Although larvae grew slightly faster when given the microzooplankton, these results still indicate that a larva could survive until an age of 10 days without the high concentrations of micronauplii that O'Connell and Raymond (1970) found to be necessary. If anchovy larvae survive to a size of 5 to 6 mm on *G. splendens*, their feeding efficiency would be higher than smaller larvae (Hunter 1972), and because of their larger size, the volume of water that larvae could search for food would also be increased. These factors would reduce the concentration of microzooplankton necessary for survival (Vlymen in press).

During several sampling periods in 1975, Lasker (in press) found that the chlorophyll maximum layer in the nearshore region of the Southern California Bight was dominated by *Gonyaulax polyedra* or a variety of small diatoms. Our work indicates that during the time periods when these phytoplankters predominated, feeding conditions for post yolk-sac anchovy larvae would be less suitable than when *G. splendens* was abundant.

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COURTSHIP AND SPAWNING BEHAVIOR OF THE TAUTOG, *TAUTOGA ONITIS* (PISCES: LABRIDAE), UNDER LABORATORY CONDITIONS[1]

BORI L. OLLA AND CAROL SAMET[2]

ABSTRACT

Courtship and spawning behavior of the tautog, *Tautoga onitis*, were observed under controlled laboratory conditions. Two separate groups of tautog, consisting of two males and one female, were each studied over an entire spawning season. The larger male of each group was dominant over the other two animals. This dominance was expressed during the spawning season by intensified aggression towards the subordinate male. The dominant male of each group, once reaching seasonal reproductive readiness, was the primary spawning partner of the female. Prior to the onset of spawning, a rapid approach of the dominant, formerly a component of an aggressive chase, functioned as a courtship behavior directed at the female. Each day the female exhibited dynamic and transient shading changes which became maximally developed as the time of each spawning approached in the afternoon. Actual gamete release, which took place each day following 6 to 8 h of courtship, occurred as the dominant male and the female moved upwards in synchrony and spawned near or at the surface. The significance of courtship and spawning in tautog is discussed and compared with reproductive behavior in other labrids.

The tautog, *Tautoga onitis*, a member of the family Labridae, occurs along the coastal regions of North America, ranging from South Carolina to Nova Scotia (Bigelow and Schroeder 1953). As with labrids in general, the fish are found associated with shelter or cover, a habit primarily related to the animals' requiring protection especially during nighttime, when they are quiescent (Olla et al. 1974).

According to previously published accounts, tautog are long-lived, reaching a maximum age of at least 34 yr (Cooper 1965) and becoming sexually mature at 3 to 4 yr of age (Chenoweth 1963; Cooper 1965; Briggs in press). The adults move offshore in the late fall to overwinter, a pattern established in field studies off Rhode Island (Cooper 1966) and off Long Island, N.Y. (Olla et al. 1974; Briggs in press). In contrast to the adults, the young remain inshore, spending the winter in a torpid condition (Olla et al. 1974).

Although a portion of the adult population remains offshore throughout the year in deep water (e.g., sports divers report finding tautog at offshore shipwrecks throughout the year), the remainder of the population moves inshore in late spring. Peak spawning activity occurs primarily in May and June (Chenoweth 1963; Cooper 1966).

From May through October adults are commonly found, especially in the midportion of their range, wherever there is appropriate cover and food supply. They are frequently seen by divers and are easily disturbed by such intrusions. The fish's reaction to divers may account for the fact that spawning in the natural environment has not been described. Spawning has also not been described under laboratory conditions. Until now the only mention of any components of a possible courtship repertoire has been by Bridges and Fahay (1968). These authors introduced a ripe male and female into a small laboratory aquarium in early June and observed transient changes in the pigmentation pattern of the female, assumed to reflect a reproductive predisposition. However, no actual gamete release was seen.

Courtship and spawning behavior in labrids has been observed in a number of species both under natural and laboratory conditions. Both paired and aggregate spawning occurs within the family. Species which have been observed to be primarily pair spawners include *Crenilabrus melops* (Potts 1974); *Halichoeres bivittatus*, *H. garnoti*, *H. maculipinna*, and *H. radiatus* (Randall and Randall 1963); *Labroides dimidiatus* (Robertson and

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Choat 1974); and *L. phthirophagus* (Youngbluth 1968). Pair spawning has also been described in *Cirrhilabrus temminckii* (Moyer and Shepard 1975), although the authors do not discount the possibility that group spawnings may occur as well in this species.

Species in which only group spawnings have been documented include *Thalassoma lucasanum* (Hobson 1965); *T. hardwicki* (Robertson and Choat 1974); and the cunner, *Tautogolabrus adspersus*, a coresident of the tautog (Wicklund 1970).

At least two labrid species have each been shown to possess both modes of gamete release. The bluehead, *Thalassoma bifasciatum*, was first seen to exhibit the dual spawning behavior under natural conditions by Randall and Randall (1963). Robertson and Choat (1974) observed similar behaviors in *T. lunare*. Both *T. bifasciatum* (Reinboth 1967) and *T. lunare* (Choat 1969) are protogynous hermaphrodites, a condition "... in which the individual functions first as a female, and later in life as a male" (Atz 1964). Although protogynous hermaphroditism is rather widespread in labrids (at least 30 species mentioned by Robertson and Choat 1974), until now only the two species mentioned above have been identified as possessing both modes of spawning.

Our aim in this work was to examine and describe the various components comprising courtship and spawning of the tautog. The studies were performed on adults which were held under laboratory conditions in a large aquarium.

MATERIALS AND METHODS

Two studies, spanning the 2-yr period of 1975 and 1976, were conducted on two different groups of adult tautog, with each group consisting of two males and a female. The fish were collected during late summer and early fall at Fire Island, N.Y., at temperatures ranging from 19° to 24°C. Scuba divers, using hand-held nets, were readily able to capture the fish at night when they are normally quiescent. The animals were easily identifiable with respect to their gender by the sexually dimorphic mandible, which is more pronounced in males (Cooper 1967).

The studies were conducted in a 121-kl, elliptically shaped aquarium, 10.6 × 4.5 × 3.0 m, located in a temperature-controlled room in which natural diurnal changes in light intensity were simulated (Olla et al. 1967). Layers of sand (0.6–0.8 mm) and gravel (2–5 mm), 0.6 m deep, provided a natural substrate for the fish. Beneath the gravel, seawater flowed through a network of pipes on the floor of the aquarium from a series of external filters containing sand, gravel, and oyster shells, and which provided continuous circulation and filtration. Water quality in the aquarium, operated primarily as a semiclosed system, was also maintained by addition of seawater from Sandy Hook Bay. The pH averaged 7.5, salinity averaged 24.0‰, and dissolved oxygen averaged 7.5 ppm.

It had been previously determined that in the natural environment a shelter area is a physical requirement of tautog, particularly during their nighttime quiescence. Shelter was, therefore, provided in the form of a triangular-shaped structure consisting of three clay drainage tiles (30.5 × 60.9 cm) cemented together. The shelter was placed approximately 3 m from one end of the aquarium in proximity to viewing windows. Clumps of live blue mussel, *Mytilus edulis* (5–17 kg), a major component of the tautog's diet (Olla et al. 1974), were introduced periodically to insure a continual food supply which allowed the fish to feed ad libitum. The mussels were placed 4 m from the shelter and constituted a more or less fixed feeding area.

Diurnal changes in light intensity from morning to evening civil twilight were simulated by banks of fluorescent lights mounted on the walls above the aquarium and controlled by a series of timers (Olla et al. 1967). A low level of night illumination, 0.75 lx was provided by incandescent bulbs, programmed to come on before the last row of fluorescent lights was extinguished.

Aquarium Conditions During Animals' Residency

Study 1

One male [51.5 cm TL (total length)] and one female (50.0 cm TL) were introduced into the aquarium on 20 September 1974, with a second male (59.0 cm TL) introduced 7 days later. From this point, the animals were kept in the aquarium for a total of 244 days. The fish were initially held at 19.1°C (+0.8°; −1.6°C) for 50 days. The animals were then the subjects of a long-term study dealing with the effects of temperature on activity and social behavior (Olla in prep.). Beginning at light

onset 51 days after the three fish were placed in the aquarium, the water temperature was increased during a 9-day period (mean rate 0.04°C/h) and held for 11 days at 28.7°C (+0.2°; −0.1°C). The temperature was then decreased over an 8-day period (mean rate 0.05°C/h) and held for 165 days from 14 December 1974 to 28 May 1975 at 18.7°C (+1.1°; −0.8°C).

During the first 10 days of the animals' residency, the photoperiod was decreased from 13.18 h to 12.25 h and then held constant through 22 February 1975. Beginning on 23 February 1975 the light schedule was set to conform with the natural, increasing photoperiod. The interval from 14 December 1974 to 16 January 1975 comprised the baseline nonreproductive period for Study 1. Observations on courtship behavior first began on 11 April 1975.

Study 2

Two males (54.0 cm TL and 55.3 cm TL) and one female (47.0 cm TL) were introduced into the aquarium on 28 August 1975 and kept in the aquarium for a total of 225 days. They were initially held at 21.3°C (+1.9°; −1.5°C) for 80 days. The animals were then the subjects of a long-term study dealing with the effects of temperature on activity and social behavior (Olla in prep.). Beginning at light onset of the 81st day of the animals' residency, the water temperature was gradually raised over a 9-day period (mean rate 0.04°C/h), held for 11 days at 28.7°C (+0.2°; −0.4°C), decreased during 8 days (mean rate 0.04°C/h), and then held for 115 days from 14 December 1975 to 8 April 1976 at 20.2°C (±0.7°C).

During the first 22 days of the animals' residency, the photoperiod was decreased from 14.23 h to 12.32 h and then held constant through 2 March 1976. Beginning on 3 March 1976 the light schedule was set to conform with the natural, increasing photoperiod. The interval from 14 December 1975 to 15 January 1976 comprised the baseline nonreproductive period for Study 2. Observations on courtship behavior first began on 29 January 1976.

Observation Schedule

Hourly observations made on the fish during the light period of each study consisted of 15-min readings. During each, the following measures of behavior (described in Results) for each fish were recorded for 50 counts in sequence at 18-s intervals: 1) number of aggressive interactions between fish and identity of aggressive and submissive individuals, and 2) number of courtship interactions and identity of participants. Qualitative aspects of behavior were also recorded during each reading.

During the nonreproductive period, 12 hourly observations (0700–1800 EST) were made daily in 4-day periods with intervals up to 3 days between periods. A total of 28 observation days (336 h) were made in the nonreproductive period of Study 1 and 20 days (240 h) in Study 2. During the reproductive period 8 hourly observations (0800–1500 EST) were made daily. In Study 1 these were taken in 2-day periods, with intervals up to 5 days between periods, while in Study 2 there were 4-day observation periods with intervals of up to 3 days between each. During the reproductive period a total of 15 observation days (120 h) were made in Study 1, and 13 days (104 h) in Study 2.

To compare differences in aggressive interactions prior to and during spawning, we selected 11 typical days of observations during the nonreproductive and reproductive periods of each study. Data based on the hourly means (0800–1500 EST) from these days are presented in tabular form in the Results.

Once we discovered that gamete release occurred in the afternoon on a daily basis and we had become acquainted with the reproductive repertoire of the animals, we could predict approximately when daily spawnings would occur. Therefore, in addition to the readings mentioned above, we also began to observe the fish at least 60 min and some days up to 150 min prior to and including each spawning. In Study 1 approximately 35 h and in Study 2, 25 h of observations were made prior to spawnings. During 11 typical spawning days, data collected in this fashion enabled us to determine quantitatively: 1) if there were any changes in aggression throughout the day as the spawning time approached, and 2) how close (temporally) to the spawnings, changes in courtship behavior were manifested.

Throughout each study and particularly prior to each spawning, observations were made with the use of a tape recorder. In addition, periodic motion pictures taken throughout the spawning period allowed us to analyze and interpret behavioral components and sequences both in slow motion and at stop frame.

RESULTS

Interactions Prior to Spawning Season

Prior to the onset of spawning in each study, there had developed a clear dominance hierarchy based on size, with the largest fish of each group, a male, being dominant over a smaller male and still smaller female. In turn, the smaller male was dominant over the female. Prior to the reproductive season, the majority of interactions among the three fish consisted of aggressive behavior. During various hours of the day the aggression, initiated particularly by the dominant male, served in part to limit the access of the subordinate male and female to different areas of the tank, such as the feeding area and shelter site (Olla in prep.).

Aggression was manifested at varying levels of intensity with the more intense involving the pursuit of a fleeing subordinate by a dominant, which we termed a chase. Prior to such an encounter a dominant often rapidly approached (swam towards) a subordinate. The subsequent chase could last as long as 30 to 45 s, with the fish swimming the length of the tank and at speeds reaching 100 to 150 cm/s. The most intense but rarest encounter involved a chase accompanied by the dominant biting a subordinate on any area of its body, which we termed nipping.

Aggressive encounters could also be quite subtle, with a subordinate exhibiting a change in its location, either vertically or horizontally, to a new position 0.5 to 1.0 m away, which we termed displacement. The behavior of a dominant causing this response often did not appear to differ from its forward swimming motion. Displacement of a subordinate occurred either as a dominant approached or simply turned towards it, as much as a full tank length away (10.6 m). Then there were instances in which a similar action of a dominant did not elicit any response by a subordinate. This variation in response by a subordinate was due to our not being able to assign an observable cause with regard to the actions of the dominant. We could only infer, through a subordinate's behavior, the generation of an aggressive intention signal by the dominant male.

Aggression by the dominant also caused a subordinate to assume a posture which we interpreted to be submissive, which involved the subordinate tilting its dorsal surface towards the dominant at an angle ranging from 5° to 90°. Frequently, when a subordinate was swimming about the tank and approaching an area in which the dominant was present, it would show the submissive posture as it bypassed and clearly avoided the dominant. The distance at which this would occur varied, ranging from 1.0 to 3.0 m.

Onset of Reproductive Period and Courtship Behavior

The most obvious manifestation of the approach of reproduction was the change in aggression directed toward the female by the dominant male. Beginning in early April 1975 (Study 1) and in late January 1976 (Study 2), a rapid approach of the male, which had previously represented the initiation of a chase, became functionally transformed into a component of the courtship repertoire. Now when the male approached, when within 5 to 10 cm, he veered off to one side or the other. The female was neither displaced nor showed any change in posture. We defined these acts of the male as rushes to distinguish them from approaches which formerly caused displacements and were aggressive. Rushes were directed at the female whether she was active or resting. At times as the male veered off, the magnitude of the water displacement from the force of the caudal thrusts was great enough to stir the adjacent sand and cause the female to be moved several centimeters. Rushes were observed approximately 2 wk (Study 1) and 7 wk (Study 2) prior to the first spawning.

The female, previously limited in her access to different areas of the tank, now was more mobile and concurrently began to show changes in her behavior towards the dominant. Sometimes immediately after the male's rush, the female followed him at a distance of approximately 0.5 to 1.0 m. The duration of the following behavior was usually short, lasting no more than 2 to 5 s. If the male did not initiate another rush, one of the pair simply swam away.

Another change in the female's behavior towards the dominant male was her resting in areas in which the dominant was resting. While in Study 2 this generally occurred along the walls of the tank or in the feeding area, in Study 1 it often focused around the shelter. On occasion when the dominant male was resting inside the shelter, the female often settled at the base of the structure, or sometimes actually entered and came to rest alongside the male within the same tube or in a different one.

While the female of Study 1 appeared to play a

rather passive role in stimulating the dominant male's attention (except when she simultaneously entered the shelter with him), the female of Study 2 was behaviorally much more conspicuous in attracting the attention of both males, particularly as they fed. On several occasions the female not only ingested mussels from the same small pile on which a male was feeding, but even wrested a clump of mussels from a male's mouth. This behavior was readily tolerated by both males.

In contrast to the termination of aggressive interactions between the dominant male and the female during this early prespawning period, the aggression of the dominant towards the subordinate male began to increase both in frequency and in intensity. In Study 1, aggressive acts by the dominant toward the subordinate rose from an average of 2.4/h during the nonreproductive period to 16.0/h in the week prior to the first spawning. In Study 2 aggressive acts rose from an average of 2.6/h during the nonreproductive period to 6.3/h in the week prior to spawning. Once daily spawning began in both studies, intermale aggression remained consistently high and was significantly greater during the entire reproductive period than during the nonreproductive period ($P \leq 0.05$; end count test; Tukey 1959; Table 1).

TABLE 1.—Comparison of aggressions by dominant male toward subordinate male *Tautoga onitis* for 11 days during nonreproductive and reproductive (spawning) periods of Studies 1 and 2. Data are presented as a mean of 8 h/day (0800–1500 EST) during nonreproduction and reproduction.

Study 1		Study 2	
No. aggressions per hourly observation per day ($\bar{x}$)	End count	No. aggressions per hourly observation per day ($\bar{x}$)	End count
Nonreproductive period:			
1.5	[1]–	3.0	–
2.8	–	2.3	–
3.5	–	3.5	–
1.8	–	2.9	–
3.3	–	2.4	–
3.9		3.3	–
3.9		3.8	–
0.9	–	1.4	–
1.9	–	2.3	–
1.1	–	2.3	–
2.0	–	1.8	–
Reproductive period:			
14.2	[2]+	10.8	+
22.4	+	10.6	+
10.2	+	10.0	+
9.9	+	7.6	+
8.4	+	12.9	+
10.2	+	14.6	+
7.0	+	12.4	+
8.8	+	20.1	+
3.5		23.5	+
3.6		26.4	+
7.1	+	26.5	+
Total end count = 18		Total end count = 22	
$P \leq 0.05$		$P \leq 0.05$	

[1]– = Values for aggression during nonreproduction smaller than smallest reproduction value.
[2]+ = Values for agression during reproduction greater than greatest nonreproduction value.

The heightened intensity of aggression was reflected by the increased duration of a chase, which commonly lasted as long as 60 to 90 s with the two fish covering anywhere from 1 to 3 circuits around the tank. In both Studies 1 and 2, the other obvious factor reflecting this heightened aggression was that the dominant began nipping and biting the subordinate during chases. As a result, each subordinate male in Studies 1 and 2 bore numerous wounds on all areas of its body.

One further piece of evidence of the increased aggression of the dominant male in each study was that the subordinate male now spent the majority of time confined to either end of the aquarium, sculling in place along the wall between middepth and the surface. These locations appeared to be the ones which elicited least aggression by the dominant male.

Along with behavioral changes, external changes in the appearance of the female were also occurring with the onset of the reproductive period. Enlargement of the gonads increased the girth of the female, resulting in a more rotund appearance. At the same time, we also noted minor changes in the female's pigmentation. While prior to this period she was generally a solid dark gray, now there was a mottled white, vertical bar or stripe down the middle of each side of the body, which we termed a "saddle." At this time, the saddle was in an early stage of development (Figure 1a) of what was to be a progression of significant shading changes taking place prior to and during each daily spawning (see below for further explanation). In addition, a pale, grayish-white patch developed in the inter- and supraorbital areas of the female, giving the appearance of eyebrows. The first observations of the female's saddle were made on 11 April 1975 in Study 1 and 29 January 1976 in Study 2.

Unlike the female, the dominant male's appearance prior to and during spawning was altered very little. The only discernible shading changes of the dominant males of both studies were the development of a light gray shading covering the entire head and opercula, and the transient appearance of faint white rays (approximately 2–4 cm long) extending outwards from the orbits of the eyes. Additionally, it appeared that the ventral portion of the maxilla and the entire mandible became a lighter, almost white, shade, with the exception of the dark pores of the mandibular lateral line canals. Otherwise the male's shading re-

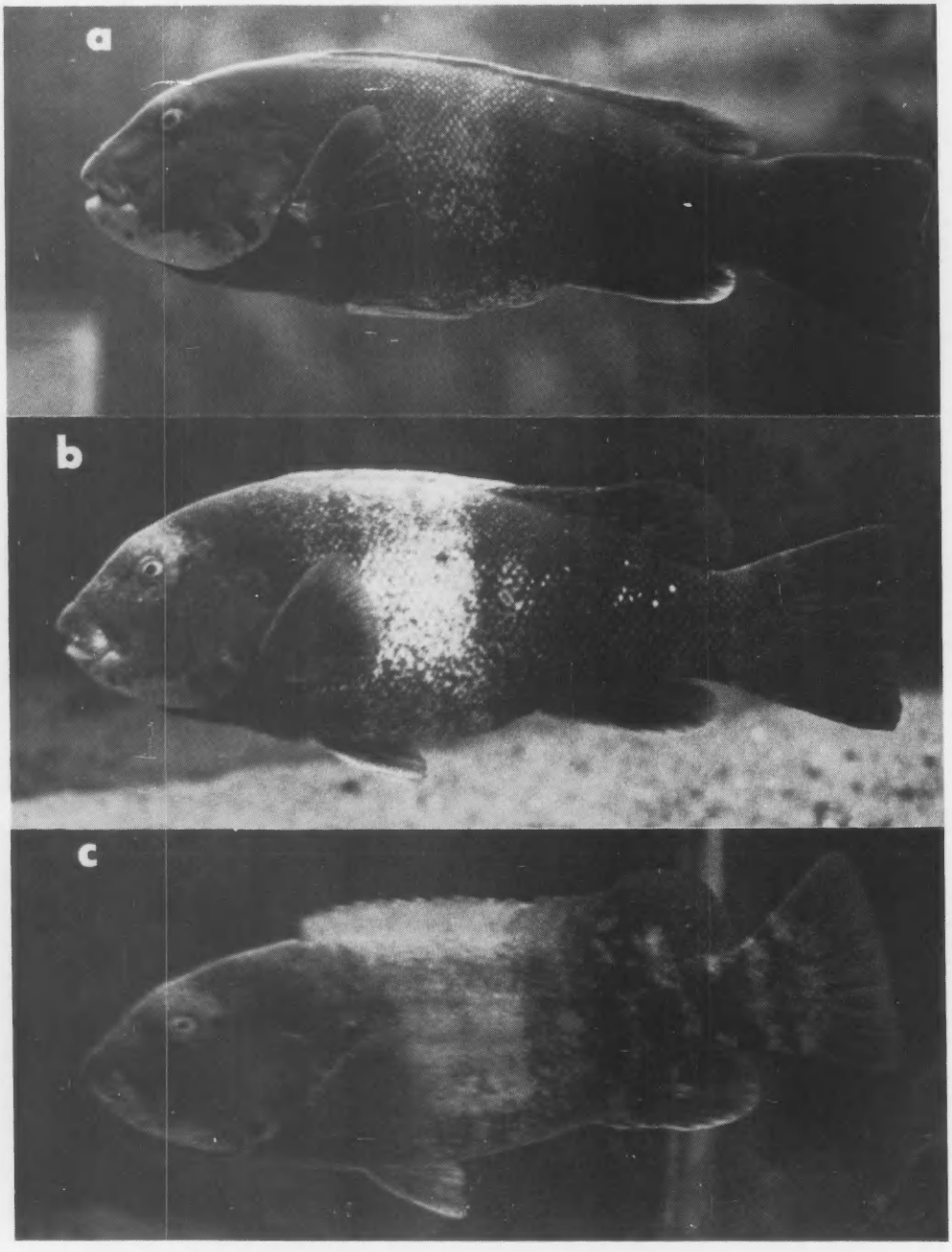

FIGURE 1.—Development of daily shading changes associated with spawning in female *Tautoga onitis*: a) earliest stage of white saddle development; b) increased size of the saddle and first, faint appearance of caudal banding as it occurs in the afternoon; c) final reproductive shading with tail-up posturing exhibited prior to spawning.

mained unchanged, with the trunk being a dark gray. Occasionally in Study 2, we noticed transient shading changes on the dominant male that were most apparent during aggression or courtship. In these cases the length of the male's midsection became a much lighter gray than the darker, dorsal area of its body. This was not a persistent change and lasted perhaps 1 or 2 min.

Development of Pair Formation

On 4 April 1975 in Study 1 (approximately 2 wk prior to the first spawning), it was apparent that there was in progress a transition from nonsexual to sexual (courtship) activities between the dominant male and female. We interpreted this to be the development of pair formation, at least within the context of the social situation and the unnatural laboratory condition.

In this same 2-wk period prior to the first spawning, the dominant's aggression directed at the subordinate male not only persisted but also began to increase and apparently served to inhibit (suppress) the subordinate's motivation to either court the female (i.e., by rushing her) and/or participate eventually in any of the spawning activities as long as the dominant was present. Since our observations in Study 1 began after courtship was under way, we were unable to ascertain the initial responses of the subordinate male toward the female, e.g., whether or not this male had originally shown any receptivity to the female (or vice versa) or attempted to court her.

In contrast to Study 1, the development of pair formation between the dominant male and female in Study 2 was slightly altered at first by the participation of the subordinate male. The dominant male had initiated rushes at the female as early as 29 January 1976 (7 wk prior to the first spawning), but then on 23 February 1976, the subordinate began to rush her periodically. In the 4-wk observation period (23 February–18 March 1976) immediately prior to the first spawning, the rushes by the dominant continued, averaging 8.8/day (range of 3–22/day), and while the rushes by the subordinate also occurred, they were lower in frequency, averaging 1.4/day (range of 0–5/day).

The events during the first and subsequent spawnings of Study 2 offered some preliminary evidence that, while gamete release was not contingent upon an established pair formation, this type of social interaction ultimately prevailed, at least under laboratory conditions. On the date of the first spawning, 19 March 1976, the female mated not with the dominant, but with the subordinate male. Although the dominant initiated some of the final courtship behavior that normally led to gamete release (see results below), and up to a point, had continued to attack the subordinate, eventually the dominant withdrew from all activities, remained inside the shelter, and did not interfere as the subordinate briefly rushed and then released gametes with the female (details described below). This type of pattern in which the dominant initiated prespawning behavior, but then withdrew and "allowed" the subordinate final access to the female for spawning persisted for 4 days through 22 March 1976.

On 23 March the dominant began taking a more active and sustained role in the final reproductive behavior. Because of this and the fact that his aggression towards the subordinate had been increasing, it appeared that the dominant might be the sole mate of the female. However, just as the dominant and female were about to spawn, the subordinate male rapidly approached the pair and simultaneously released his gametes with theirs. This pattern in which the dominant initiated and completed the spawning activities with the female, but still had not sufficiently inhibited a simultaneous spawning release by the subordinate male persisted for 7 days through 29 March 1976.

It was not until 30 March, 11 days after the first gamete release, that the spawning was completed exclusively by the dominant male and the female. Throughout the remainder of the study, the female mated exclusively with the dominant male.

Daily Reproductive Behavior

All spawnings that were observed during both Studies 1 and 2 occurred between 1330 and 1600 (EST) with the exception of one at 1015 (EST) in Study 1. The first spawning of Study 1 was on 21 April with 36 subsequent spawnings observed (1–3/day), and in Study 2 the first spawning occurred on 19 March 1976 with 22 subsequent spawnings (1–2/day).

Throughout the morning of a typical day when spawning was to occur, the dominant male was generally active, swimming about the tank, feeding, and intermittently rushing the female. Aggression towards the subordinate male usually oc-

curred right up until and after each spawning. The subordinate male continued to be restricted in its movements by the heightened aggression directed towards it and remained almost exclusively at either end of the tank, usually in midwater. The female, besides showing a minimal change in shading (i.e., early saddling, Figure 1a), as well as an occasional responsiveness to the dominant, also engaged in activities not directly related to spawning, such as feeding, swimming (with no apparent interactions with the other animals), and resting.

While the female either briefly followed after and/or rested near the dominant or exhibited no response to the rushes prior to this period, as the morning progressed she responded with progressive shading changes of varying magnitude. For example, within several seconds after a vigorous rush by the dominant male, the saddle oftentimes increased in depth and width. On some occasions the saddle took on a pale yellowish hue. The anterior half of the dorsal fin became a mottled white, ending at the same posterior border as the saddle. In addition, faint, white vertical stripes became evident on the caudal areas of the body, originating at the posterior edge of the saddle and extending just past the caudal peduncle (Figure 1b), similar to that described by Bridges and Fahay (1968). The pattern could vary, with these stripes modified into a kind of checkerboard. Along with this shading, the female often erected her dorsal fin very briefly (1–2 s) immediately following a rush.

Unless spawning was imminent, i.e., occuring within 15 to 30 min, these shading changes in the morning were retrogressive. A particular pattern might not last for more than 10 to 20 s or, at the longest, several minutes, followed by fading, with only a thin saddle persisting.

During the afternoon as the time of spawning approached (30–60 min prior to spawning), the dominant male became more responsive to the female, as evidenced by the increased intensity of the rushes. As these continued the female began to erect the dorsal fin for progressively longer periods, anywhere from 5 to 15 s. During fin erection the total area of white spanning the saddle and the dorsal fin was now maximized and, we believe, served to increase the female's conspicuousness.

In this same period she began to swim at times only with the pectorals and also intermittently began to flex the caudal fin upward. When caudal flexion first began, it usually followed a rush and was accomplished by a series of small lifts in which the female raised the caudal fin progressively higher.

The responsiveness of both the male and female was at its peak for the 15 min prior to spawning. While the number of rushes during each of the 15-min hourly observations throughout the day averaged 1.2 (Study 1) and 3.3 (Study 2), the number of rushes in this 15-min period preceding a spawning increased to an average of 6.4 (Study 1) and 9.4 (Study 2). Aggression by the dominant towards the subordinate male was not significantly different between morning and afternoon for Study 1 ($P>0.05$), but increased significantly in the afternoon of Study 2 ($P\leq0.05$; sign test; Dixon and Mood 1946; Table 2).

During the 15-min period prior to spawning, the saddle of the female was almost maximally developed, appearing whiter than it had been earlier in the day, and extending fully down the abdomen. The caudal checkerboard or striped pattern was now much more clearly defined. In addition the vent began to dilate.

The behavior of the female also began to change. She was now more active, and often swam by using only the pectoral fins. When the male moved rapidly towards her in a rush, she often erected the dorsal fin and flexed the caudal fin before the male had reached her rather than afterwards. The duration of the upward caudal flexion continued to increase. Accompanying the caudal flexion was the forward tilting of the body at about a 20° to 30° angle, serving to expose maximally the dilated vent.

TABLE 2.—Sign test comparing mean number of agressions per hourly observation by dominant male towards the subordinate male *Tautoga onitis* during the morning (0800–1100 EST) and the afternoon (1200–1500 EST) on 11 spawning days of Studies 1 and 2.

Study 1				Study 2			
Date 1975	0800–1100	1200–1500	Sign test	Date 1976	0800–1100	1200–1500	Sign test
4/28	17.0	11.5	−	3/24	10.2	11.2	+
4/29	24.2	20.5	−	3/25	8.0	13.2	+
4/30	4.5	16.0	+	3/29	5.8	14.2	+
5/1	8.8	11.0	+	3/30	6.8	8.5	+
5/2	7.5	9.2	+	3/31	9.2	16.5	+
5/3	7.2	13.2	+	4/1	12.5	16.8	+
5/6	8.2	5.8	−	4/2	8.2	16.5	+
5/12	9.8	7.8	−	4/5	14.5	25.8	+
5/13	4.0	3.0	−	4/6	15.5	31.5	+
5/19	2.5	4.8	+	4/7	21.2	31.5	+
5/20	3.8	10.5	+	4/8	16.0	37.0	+
No. of +			6				11
No. of −			5				0
Difference			1				11
P			>0.05				≤0.05

Beginning anywhere from 2 to 5 min before spawning, the female began swimming back and forth along the length of the tank close to the sand using only the pectoral fins, a behavior we defined as a run. A run was usually accompanied by a full and constant erection of the dorsal fin and the final shading development in which all of the white areas of her body (i.e., the saddle, caudal stripes or white portions of the checkerboard pattern, the "eyebrows," and the anterior half of the dorsal fin) were almost totally blanched, sometimes colored with a yellowish hue. Then, as a run was either beginning or in progress, the caudal fin was rigidly flexed upward one final time (Figure 1c), exposing the maximally dilated vent, while at the same time the head was tilted downward. The female's swimming in this position seemed awkward, resulting in her moving with a characteristic wobble or wiggle. The female made one or two runs alone which apparently served to heighten the attention of the dominant male, for he would break off other activities (e.g., chasing the subordinate male, swimming randomly about the tank) to usually rush her first and then to follow her (Figure 2a).

As the female continued on the runs, the male tended to swim more in a parallel alignment with her. Eventually he swam just slightly behind with his head moving closer to the female's operculum or midsection, 30 to 40 cm away from her (Figure 2b). Then suddenly, while increasing her speed by changing from pectoral swimming to caudal thrusts, the female swam rapidly toward the surface, with the male immediately accelerating in a similar manner to keep apace with her (Figure 2c). The angle of their ascent was anywhere from 40° to 70°. When the fish were less than a meter from the surface and while still swimming rapidly, they turned their bodies so that their ventral areas faced toward each other. On those occasions when the fish's movements were perfectly coordinated, the pectorals of the male appeared to be embracing the female (Figure 2d). With the animals in contact, they arched their bodies into U-shapes and released gametes either before reaching the surface or as they broke the surface (Figure 2e). Then the pair separated and swam downwards (Figure 2f), with the female coming to rest on the sand where the male usually rushed her 2 or 3 times within 5 to 10 s following the spawning. After a spawning, the female's shading usually regressed to just a thin saddle within a few minutes.

The spawning as we have described it appeared to comprise the prevalent mode of gamete release. However, there occurred slight variations in the

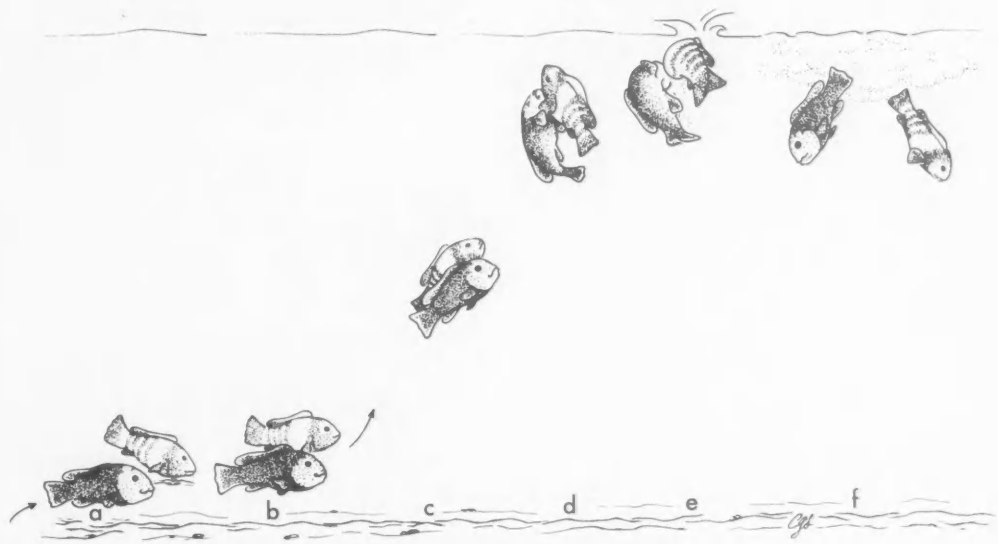

FIGURE 2.—Final sequence of behaviors leading to spawning in *Tautoga onitis*: a) male approaches female; b) they swim parallel with female slightly ahead; c) male and female move upwards in the water column; d) the pair orient to each other in a ventral-to-ventral alignment; e) with bodies flexed the pair release gametes as they break the water surface; f) the fish separate and move downwards.

behavior which still resulted in gamete release. For example, as the female was moving to the surface, rather than orienting the ventral area of her body toward the male, she bent her body into the U-shape with the result that her dorsal side faced the ventral side of the male. Gamete release still occurred as the fish flexed their bodies into U-shapes. The origin of this variation was usually due to the fact that while moving upward the female was swimming too rapidly to assume the proper alignment for the ventral-to-ventral release with the male.

A critical factor for maximizing fertilization was the breaking of the water surface at the time of release. As the fish moved upwards, churned the water, and swam downwards again, currents were created which mixed the "cloud" of gametes together. From visual observations and motion picture analysis, this occurred whether there was ventral-to-ventral or ventral-to-dorsal alignment of the pair. We would assume, however, that the most efficient method for fertilization involved the ventral-to-ventral alignment.

While runs were always performed prior to spawning, on some days there were as few as 2 runs prior to a spawning, while on other days there were as many as 11. Similarly, the duration of a series of runs varied from 30 to 180 s.

Runs were not always performed in succession. Particularly in Study 1, many times after completing one run, the pair began circling around each other in midwater. In some cases they followed each other, head to tail, along the perimeter of an imaginary circle. In other cases, as the male swam around the female, she either remained sculling in a fixed position or pivoted about her vertical axis, obviously orienting to the moving male. The total number of separate circling bouts during a run sequence ranged from 2 to 10 with a duration of each ranging from 2 to 40 s.

Occasionally at the end of a run, the pair began to swim upwards, as if to spawn. Typically, at the onset of this, the female began the transition from pectoral swimming to caudal thrusts. Moving rapidly upwards with the male alongside, the female broke away from him short of the surface and swam downwards to the sand without releasing gametes. This behavior sometimes did not occur at all while in other cases it occurred as many as six times prior to a spawning.

The continuity or fluidity of the run sequences appeared to be a critical factor serving to synchronize the fish for final release of gametes. Lack of mutual stimulatory behaviors or even slightly inappropriate behavior by one of the mates during a run, in general, were sufficient causes for a temporary breakoff of the entire sequence. During a breakoff the female's shading often regressed somewhat and she came to rest on the sand or even returned to the shelter for a few seconds.

One of the specific causes for these breakoffs was due to the fact that the dominant male, instead of maintaining his attention toward the female, chased or displaced the subordinate male which had either (actively) moved too close to the pair or (passively) happened to be in areas where the prespawning behavior was being carried out.

Other reasons for the breakoffs were inappropriate stimuli initiated usually by the male during the run sequence. In Study 1, if the male contacted the female during a run along the sand or as she ascended to spawn rather than at the apex of the pathway, the female often turned away from the male. Conversely, premature contact behavior by the male in Study 2 was an appropriate stimulus to his mate and in fact was frequently exhibited during the run sequence as well as during spawning.

Other cases in which the female initiated a breakoff from a run occurred if the male assumed an atypical position relative to hers. In Study 1, the female usually swam between the wall and the male and slightly ahead of him. Occasionally if the male assumed the position closest to the wall during a run (i.e., the female was now closer to the center of the tank) or if the male swam ahead of her, the female broke away. Since the male sometimes "corrected" his position relative to hers and hence the female did not break away, it appeared that each animal had become conditioned to a rather stereotyped set of behavioral patterns and positions which facilitated bringing the spawning to completion.

Reproductive Behavior of the Subordinate Male

In both studies each subordinate male had achieved gonadal maturation and was able to complete spawning with the female under a limited set of conditions. In each case, the reproductive behavior occurred only when the subordinate was not behaviorally inhibited by the dominant male. In Study 1, the first spawning by the subordinate male and the female occurred later in the spawning season, on the very day (29 May 1975)

that the dominant male was dying (unknown causes). This latter animal was obviously in a weakened condition and did not participate or interfere with the reproductive activities during his last day of survival. In Study 2, as described above, the subordinate male initiated courtship and spawning with the female at the onset of the reproductive season and continued until the aggression by the dominant literally suppressed all of his normal behavior.

The behavior exhibited by each subordinate male immediately prior to and during spawning was essentially comparable to that of the dominant, except that it was less stereotyped. Sometimes during a run the subordinate male weaved from one side of the female to the other; and in other cases he actually swam ahead of her on the first and second runs. Gradually as the male came to align himself more with her position, the male initiated flank contact, and positioned his body slightly above hers.

In both studies, once this continuous contact by the subordinate male was maintained, the runs, as discrete behavioral patterns, were no longer discernible. Generally the pair swam in a meandering, zig-zag pattern in midwater, and eventually circled approximately 0.5 to 1.0 m below the surface. During this behavior, it always appeared that the male was herding the female. Generally, because the pair was now so close to the surface, the final movement upwards covered only a short distance.

The subordinate male of Study 1 was last observed to spawn with the female on 25 July 1975, comprising an estimated total of 57 spawning days for this pair. Conversely, the subordinate male of Study 2 completed only 4 days of exclusive paired spawning with the female before the dominant male took an active role in the reproductive activities.

DISCUSSION

It is well known that light and temperature play a role via the neuroendocrine system in both initiating and synchronizing reproduction in fish (see review and discussion by de Vlaming 1974). However, spawning occurred in the laboratory even though the fish previously had been exposed to an unnatural photoperiod and temperature. Temperatures were, in fact, at high, stressful levels. It is possible that the endocrinological events associated with gonadal recrudescence may have been initiated 8 to 10 mo or more before the fish were captured. The photoperiod in the laboratory was eventually lengthened and regulated to keep apace of the natural changes beginning 16 days (Study 2) to 56 days (Study 1) before the first spawning. Temperatures of 18° to 20°C, well within levels at which eggs have been found in nature (Perlmutter 1939; Williams 1967), were maintained 93 days (Study 2) to 126 days (Study 1) prior to the onset of spawning.

Previously published field observations indicate that tautog spawn sometime between May and June in the waters of New York (Olla et al. 1974; Briggs in press) and Rhode Island (Chenoweth 1963; Cooper 1966), with June being the principal spawning month in Massachusetts waters (Kuntz and Radcliffe 1917; Bigelow and Schroeder 1953). These spawning dates are supported by data based on collections of eggs and larvae from Sandy Hook Bay estuary (Croker 1965) and are further extended through mid-August based on similar collections from Long Island Sound (Wheatland 1956; Richards 1959).

That the fish spawned earlier in the laboratory than they would have in nature supports the supposition that the final synchrony may depend on proximal environmental cues. While the gonadal recrudescence may have been initiated by events occurring in nature prior to capture, final synchronization may have been caused by the changes in temperature and the advancing photoperiod. Because the study was not designed to examine such questions, assignable causes of the spawning occurrence must be conjectural. Nevertheless, whatever the causative environmental events, the animals did achieve reproductive synchrony.

To date there are no specific descriptions of spawning behavior in the tautog. In a laboratory study on tautog in June 1967, Bridges and Fahay (1968) reported that during a 10-day period, a ripe female and male both underwent a shading change between 1500 and 1630 and exhibited behavior which the authors described as possible courtship. Our observations concur with these authors with respect to the daily afternoon shading alteration of the female. However, their descriptions of the behavior suggested aggressive interactions between the two animals and thus the male's shading more likely reflected an animal involved in aggression rather than courtship. The female and male's behavior further suggest that

either the animals were not in complete reproductive synchrony or the confines of the aquarium may have produced behavioral artifacts.

In our studies, pair spawning, with the dominant male tautog being the exclusive partner of the female, was the prevalent mode of reproductive activity. However, in Study 2 when spawning began, the female spawned first with the subordinate male, then both males, and finally only with the dominant. This transition period, we surmise, may have been caused by either or both of the following: 1) due to the small difference in size (1.3 cm) between the males, dominance may not have been sufficiently defined initially to inhibit the subordinate, and 2) the final phase of seasonal reproductive readiness of the dominant was slightly behind that of the subordinate. Once the dominant reached an appropriate level of sexual maturation, pair spawning involving only the dominant male and the female occurred exclusively for the remainder of the study.

Pair spawning again proved to be the mode of gamete release in our laboratory facility when a single male was in the presence of two gravid females (Olla and Samet unpubl. data). In July 1976 these two females (approximately 48 and 58 cm) were introduced into the aquarium where the dominant male from Study 2 was still residing. During intermittent observations of the fish, pair spawning occurred five times with the smaller female, although both females were rushed and exhibited a high degree of attention towards the male.

While we have never seen tautog spawning under natural conditions, it is reasonable to assume from our observations that pair spawning may play a leading role in the reproductive repertoire of this species. However, we reserve judgment as to whether this is the only pattern of gamete release, especially because of the occurrence in Labridae of both paired and aggregate spawnings within a single species, e.g., *Thalassoma bifasciatum* (Randall and Randall 1963) and *T. lunare* (Robertson and Choat 1974), both of which are protogynous hermaphrodites (Reinboth 1967 and Choat 1969, respectively).

Another factor contributing to our reserve in assigning only one pattern of reproduction to tautog is that during recent preliminary field studies, Olla and Bejda (in prep.) found sexually mature young tautog, both males and females, which were of a much smaller size and younger age than has previously been reported (Chenoweth 1963; Cooper 1966; Briggs in press). In addition, these young fish did not show sexual dimorphism of the mandible (Cooper 1967), a characteristic trait which was conspicuous in the subjects used in our studies. One explanation for the absence of the mandibular dimorphism in these young fish might be that this trait occurs in older, larger fish. Although we do now know yet whether the young animals participate in spawning, the other possibility is that these fish may represent a different sexual stage than that of the older fish of our study. It is even possible, as remote as it seems, that hermaphroditism may be present. The question is raised here because we know nothing of the behavior or gonadal development of these young fish and because hermaphroditism, in the form of protogeny, has been found in a number of labrids (e.g., 30 species according to Robertson and Choat 1974).

While it appeared that pair formation did take place within the laboratory, whether or not a true pair bonding between mates occurs in nature is still unanswered. It is possible that in their natural environment, other male tautog in the vicinity of a pair could conceivably participate at the moment of spawning. However, in these circumstances it is also quite possible that the extreme aggression of a dominant, courting male would cause other subordinate males to remain sexually passive or to move away and seek a female partner elsewhere. The hypothesis that within a given locale a dominance hierarchy among males determines which male becomes sexually active is supported by a field experiment on *Thalassoma bifasciatum* by Reinboth (1973). Additionally, it is quite possible in a natural environment that a female might spawn each day with a different male.

On the other hand, if true pair formation solely between one male and a female is possible, the selective advantage here is obvious, inasmuch as 1) it would not be necessary for an animal to expend energy finding a mate each day, and 2) to sustain its dominance (and pairing with a female) the male must continue to be a highly successful competitor. When the motivation to spawn wanes, males capable of becoming sufficiently dominant over others would have priority to act as mates.

Of all the sensory stimuli that could potentially come into play during tautog courtship, visual cues arising from the female appeared to be the most conspicuous. First, the swollen, gravid abdomen of the female, which as Youngbluth (1968)

studying the cleaning wrasse, *Labroides phthirophagus*, and Potts (1974) studying the corkwing wrasse, *Crenilabrus melops*, suggested, may have served as one of the first important visual cues to the male. In addition, the development of the female tautog's saddle, even in its most rudimentary state 2 to 7 wk before the first spawning of each study could have played an important role in identifying the reproductive state of the female. More specifically, the daily transient changes in the saddling would have served to identify the readiness of the female to spawn right up to the moment of spawning.

The existence and development of reproductive shading patterns in the female tautog is in distinct contrast with the situation found in other labrids in which the conspicuous or bright appearance, when present, is usually found in males (see Roede 1972, for review and discussion). Substantiation of the female tautog's spawning pattern was made during an observation with scuba at approximately 1500 (EST) on 26 May 1976 near the Fire Island Coast Guard Station. An adult, gravid female (approximately 45–50 cm) with a well-developed saddle was observed swimming in midwater along with a dark gray male (A. D. Martin pers. commun.). (Turbidity and the fact that the pair moved away from the diver prevented any further observations.)

Another major difference between tautog and other labrids regarding coloring or shading is that the shading change of the female was a dynamic, transient process each day. This kind of shading change in tautog falls within the category of physiological color changes discussed by Roede (1972), which reflect rapid alterations in shading and which are also reversible processes. Conversely, the descriptions of color patterns in other labrids all appear to reflect morphological color changes, which develop only gradually within each individual and particularly within discrete life phases or stages.

In concert with these shading changes were actions of the female that apparently served to enhance or facilitate the male's perception of these visual stimuli. For example, the final sustained erection of the female's dorsal fin further enlarged the white area of the saddle. Lifting of the female's caudal fin, occurring when the saddle and caudal pattern were maximally developed, was manifested in the final moment before spawning. This lift, coupled with the female's swimming near the male in such a fashion as to expose the dilating vent, provided another stimulus towards which the male could orient.

Visual shading cues arising from the dominant male appeared to be minimal except perhaps for the lightening of its face and lips. These features may have provided a stimulus to the female indicating the male's motivation to court and spawn, particularly during rushes directed at the female's head. The stimulus value of the male's white lips during courtship displays in *Crenilabrus melops* has also been suggested by Potts (1974).

The obvious visual cues of the male, arising from its rapid approach during a rush, were quite likely a primary source of stimulation to the female. It is also possible that there was a secondary, lateral-line stimulation, created by the force of the water currents as the male rushed by and which may have enhanced the overall response of the female. Other potential stimuli arising from either of the mates may have been chemosensory in origin. We have no basis at this point to conjecture whether or not the animals released and/or perceived any chemical products (i.e., pheromones), which may have functioned to facilitate reproduction.

An important indicator of the approaching onset of the reproductive season was the change in behavior of the dominant male towards the female. It gradually ceased being aggressive to the female, initiated courtship rushes, and permitted her unrestricted access to any area of the tank. This behavioral transition from aggressive to courtship activities is very similar to that observed in *Crenilabrus melops* (Potts 1974). In this species, which pair spawn at a nest site, the nesting male is aggressive to both males and females at the onset of the reproductive period. Eventually, however, instead of approaching a female to chase or bite her, the male performs an exaggerated courtship, swimming around the female which apparently stimulates her to approach the male and his nest.

As with many other species, each of the courtship activities of the tautog seem to serve one major purpose, which was the gradual excitation and synchronization of the partners prior to the spawning each day. In the extended period before the very first spawning of the season, the dominant male appeared to assume the more physically active role in the early courtship, primarily by rushing the female. While the female did occasionally follow after or rest near him, she did not perform any obvious (ritualized) activities. Nevertheless, even the slight shading changes in

her saddle during a rush may have functioned as a type of response, communicating to the male her receptivity and possibly her altering physiological state.

Once the first and subsequent daily spawnings began, it appeared that the female now set the tempo for synchronizing the events leading to spawning. The first "signal" that spawning was imminent occurred when the female's caudal stripe or checkerboard pattern was consistently maintained, followed by a further broadening and blanching of her saddle. Then, once her pectoral swimming, the tail lift, and head-down behaviors were sustained, the female initiated the final courtship behavior (i.e., runs). Even though the male synchronized his movements with hers, the pace and completion of the runs and upward spawning motion were contingent on the female's actions.

The separate behavioral components of the courtship and spawning repertoire in the tautog reflect both similarities and differences when compared with other labrid groups. In the cleaning wrasse, *Labroides phthirophagus*, pair formation and courtship precede spawning by at least a week or more (Youngbluth 1968). During this time the male repeatedly performs rapid approaches ("passes") towards the side of the female which she tolerates; however, the male's action in this case is generally also accompanied by a body quivering. In some species the only vigorous approaches by males toward females are described as chases, such as in the four *Halichoeres* species observed by Randall and Randall (1963); the cunner, *Tautogolabrus adspersus* (Wicklund 1970); *Thalassoma bifasciatum* (Randall and Randall 1963); and *T. lunare* (Robertson and Choat 1974). In *Cirrhilabrus temminckii* the male performs a single rushing action similar to the tautog, but this only occurs immediately prior to the upward darting for gamete release (Moyer and Shepard 1975).

In many of the species described above, the males also perform ritualized swimming patterns or displays to attract the females. These have been described as circling, looping, fluttering, dancing, or simply courtship swimming. The responses of females among the various species can vary from a simple approach such as in *T. bifasciatum* (Reinboth 1973) to an over, reciprocal response such as "sigmoid posturing" and "dancing" as in *L. phthirophagus* (Youngbluth 1968), or a lateral approach to the male in which the swollen flank and genital papilla are presented as in *Crenilabrus melops* (Potts 1974).

With the exception of *C. melops* which spawn on the sand in a nest, all of the other species mentioned above and tautog share a common mode of swimming or darting rapidly upwards to spawn. Body bending (only by the male of a pair) in *T. bifasciatum* has been observed by Reinboth (1973) as well as the brief alignment of the pair's genital openings.

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DISTRIBUTION, SIZE, AND ABUNDANCE OF MICROCOPEPODS IN THE CALIFORNIA CURRENT SYSTEM AND THEIR POSSIBLE INFLUENCE ON SURVIVAL OF MARINE TELEOST LARVAE[1]

DAVID K. ARTHUR[2]

ABSTRACT

The California Current system can be divided into onshore and offshore faunal zones by a copepod indicator species, *Mecynocera clausii*. Near the outer edge of the onshore zone copepod nauplii densities were higher than usual. There were about 3 times as many microcopepodids and 12 times as many nauplii on the average throughout the onshore as in the offshore zone. Feeding habits of larvae of sardines, anchovies, and jack mackerel may be adapted to the usual naupliar and copepodid concentrations of the zone in which they were spawned. The usual concentration of 56-μm and wider nauplii in the onshore zone was about 3/liter with 17/liter the highest observed which indicates that for nauplii of all sizes there were usually about 36/liter and with the highest density of 195/liter. These concentrations are lower than has usually been reported to be required for rearing larval fish in laboratories. Numbers of nauplii decreased exponentially with increasing size but a naupliar biomass maximum was found to occur at about the 70 μm width. Nauplii of this size are ingested at first feeding by Pacific sardine, northern anchovy, and jack mackerel larvae. It is suggested that larval feeding habits of these fish have evolved to utilize this important food resource at their first feeding.

Copepods form the bulk of most zooplankton hauls from the sea and are important because they are the main convertors of phytoplankton into food suitable for higher organisms (Marshall 1973). Copepods are especially important as food for planktonic larvae of pelagic marine teleosts. Food of the larvae of commercially important marine fishes has been widely reported as being primarily eggs, nauplii, and copepodid stages of small copepods. Yokota et al. (1961) found that food occurring in the feeding larvae of all the 57 species taken in their primarily coastal samples was almost entirely small copepods, especially nauplii. Duka and Gordina (1973) investigated the food of larvae of 26 species of teleosts from the Mediterranean and adjacent areas of the Atlantic and reported that copepod nauplii composed 90% of all items eaten by small larvae (2.3 to 5.0 mm). Stomach content analyses of fish larvae are also corroborated by population dynamic studies of plankton organisms. Fish (1936) noted that in the Gulf of Maine a small copepod, genus *Pseudocalanus*, suffers a much higher predation rate during the naupliar stages than does *Calanus finmarchicus* whose eggs (140 μm wide) and nauplii are too large to be ingested by many fish larvae.

When it became apparent that the population of Pacific sardine, *Sardinops sagax*, was in serious decline, a research program [later to become known as CalCOFI (California Cooperative Oceanic Fisheries Investigations)] was initiated in 1949 to investigate the ecology of this important fish. One part of this investigation was a study of the food and food resources of sardine larvae and consisted of two main objectives: 1) determine what the larvae eat, and 2) to study the abundance and distribution of these food items. The ultimate purpose was to determine if feeding conditions, especially for the first feeding larvae, could be a contributing factor to the sardine's decline, as was proposed by Hjort (1914) to explain poor year class survival of fishes in general.

The identifiable food of first feeding sardine larvae was primarily copepod nauplii ranging from 25 to 80 μm but mostly about 70 μm wide (Arthur 1976). Nauplii of this size are produced only by small species of copepods, roughly less than 1.5 mm long. The assemblage of these small copepods is composed of many species. Several genera have often been recorded as being abun-

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dant in the plankton as well as in the intestinal contents of larval fishes. Among these are the cyclopoid genus *Oithona*, (especially *O. similis*), and the calanoid genera *Pseudocalanus* and *Paracalanus*. *Oithona similis*, whose first stage nauplius is 70 μm wide (Oberg 1906) and can, therefore, be ingested by sardine larvae, composed over 50% of the cyclopoid fauna in 37 of the 42 samples off Oregon through Baja California examined by Olson (1949). Because of the large number of species, many of whose developmental stages had not been described, no attempt was made in this study to identify eggs, nauplii, and copepodid stages to species.

This report deals with size, abundance, and distribution of naupliar and copepodid stages of copepods captured with relatively fine meshed plankton samplers in and near the California Current. These small species of copepods will be referred to as microcopepods, and all postnaupliar stages, including adults, as copepodids. The term nauplii will include true nauplii and metanauplii.

SAMPLING METHODS

The need for a study of the small crustacean plankton was anticipated early in the CalCOFI program. The 1-m net with its relatively coarse mesh (505 μm) was considered adequate for sampling sardine eggs and large copepods and euphausiids, but most small copepods and nauplii pass through this size mesh. Starting in May 1949, a Clarke–Bumpus sampler (Clarke and Bumpus 1940) equipped with a #8 mesh bolting silk net, (203 μm in unused condition) was used routinely at stations in the central and upper southern California areas. It was towed obliquely from a depth of 70 m, filtering about 5 m^3 of water.

The Clarke–Bumpus sampler was abandoned after March 1950 in favor of the "high-speed sampler" (California Academy of Sciences et al. 1950) which was modified by having a mouth diameter of 7.6 cm, the same as the main fuselage of this device, rather than being tapered to a narrower opening as in the original high-speed sampler. It was equipped with a 143-μm wire filter and was towed on the same wire as the meter net and was used because the record it made of depth versus volume of water filtered could be used to analyze the meter net track as well as its own. This modified version was called the "microplankton sampler." It was towed obliquely from a depth of 70 m during March 1950–September 1950 and from 130 m on cruises from November 1950 to July 1952.

After a study had been made of the food ingested by ocean-caught sardine larvae, it became obvious that very small copepod nauplii are critical in the ecology of these larvae. Therefore, after August 1951 a plankton sampler of much finer mesh was used. This sampler was essentially a medium Epstein net (Sverdrup et al. 1942:379) with a mouth opening 17.5 cm in diameter, connected by a canvas collar to a filtering cone constructed of #20 bolting silk (76 μm in unused condition). This sampler was hauled vertically from a depth of 50 m and was called the "truncated net."

These three plankton samplers were used between May 1949 and September 1954. Pertinent statistics are compared as follows:

Sampler	*Mouth diameter (cm)*	*Mesh aperture size (μm) New*	*Used*	*No. of samples*
Clarke–Bumpus	12.5	203	120	185
Microplankton	7.6	143	143	612
Truncated net	17.5	76	56	239
				1,036

Because of expansion when wet, and the unraveling of threads when used, the aperture size of used wet silk nets is considerably smaller than new dry ones. The above "used" values were obtained by measuring aperture sizes, when submerged in water in the laboratory, of nets being used in the collections. Even with the smallest aperture size used (56 μm) many nauplii and copepodids must have escaped. Beers and Stewart (1967) reported that a significant quantity of copepods pass through a 35-μm mesh. Most food particles of sardine, anchovy, and jack mackerel larvae, however, are wider than 56 μm (Arthur 1976.)

COUNTING METHOD

The plankton samples were examined in a plastic chamber measuring 60 mm by 70 mm, the floor of which was lined every 5 mm to form a grid. Its total fluid capacity is approximately 50 ml with a water depth of about 12 mm. In practice, the fluid volume in the chamber measured less than half of this. If the amount of material in the sample was not too great, the entire sample was counted. Most samples taken with the Clarke–Bumpus and truncated nets contained so much material that subsampling was necessary. This

was accomplished by first measuring the total fluid volume of the sample, then stirring it vigorously to disperse the material, then drawing off a convenient amount for examination, and finally measuring the remainder in order to determine what percentage the subsample was of the original sample.

FAUNAL AREAS IN THE CALCOFI SECTOR

Although the primary purpose of the microplankton program was a quantitative appraisal of the microcopepod fauna, a few prominent copepod species were routinely recorded. One of these, *Mecynocera clausii,* proved useful as an indicator organism allowing the CalCOFI sector to be roughly divided into two plankton faunal areas, onshore and offshore.

Mecynocera is a monotypic genus. It can readily be distinguished from other copepods by its exceptionally long first antennae (Mori 1964). Its small size (about 1 mm) places it within the microcopepod range. These attributes make it convenient and useful as an indicator of conditions affecting the microcopepod fauna. *Mecynocera clausii* has been reported near the surface throughout tropical areas of the oceans, as well as in temperate areas such as the Mediterranean. In the CalCOFI area its presence may be considered as indicating the more tropical offshore and southern waters.

A typical distribution of *M. clausii* off southern California and off northern and central Baja California is illustrated by data for February 1951 (Figure 1). *Mecynocera* is characteristic of offshore water whereas the occurrence of plutei of benthic echinoderms may indicate coastal water. The two boundaries tend to interdigitate, which must imply alternating tongues of warm offshore water penetrating toward the coast and jets of cold onshore water moving out to sea. The 15°C isotherm supports this interpretation.

Submergence of the water of the California Current under the offshore subtropical water may be indicated at stations where *Mecynocera* and plutei were taken together. This would result if the net in its 130-m deep track caught *Mecynocera* near the surface and plutei at some depth where the submerging water had carried them.

The shoreward boundary of *Mecynocera,* as determined by the various cruises, is presented in Figure 2. In general, the average boundary is found about 400 km offshore in the San Francisco area and inclines toward the coast farther south. In the northern Baja California area it may impinge upon the shoreline, but it becomes erratic in the turbulent Punta Eugenia area.

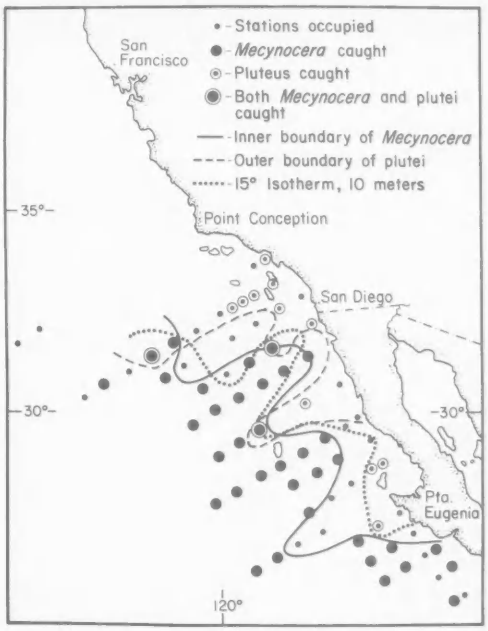

FIGURE 1.—Distribution of *Mecynocera clausii* and pluteus larvae during CalCOFI cruise for February 1951 off California and Baja California.

ZONE OF COPEPOD NAUPLII MAXIMUM

For a given cruise, if each line is examined and the station which contained the greatest concentration of nauplii is circled and the circled stations for the various lines are connected, one obtains a line of maximum copepod nauplii concentrations. Figure 3 presents a typical distribution of copepod nauplii and their maximum zone in the Channel Island area. Two stations have been circled for the line extending offshore from San Diego. It is common to find a high local concentration at stations near the coast and a second high offshore particularly in the area north of Point Conception. Had the station pattern extended closer to the beach, higher concentrations of nauplii probably would have been encountered there. During a 5-mo

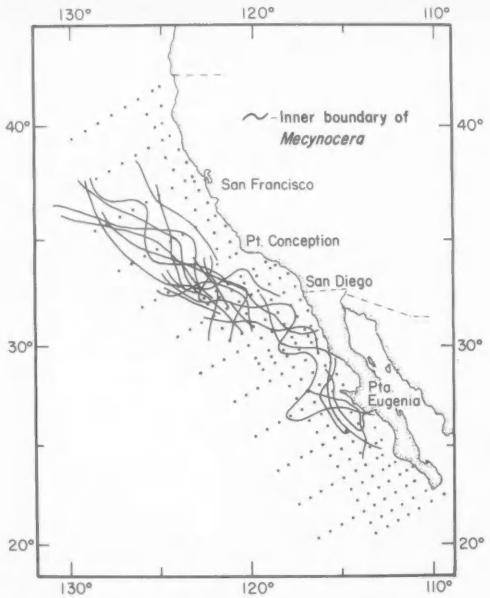

FIGURE 2.—Inner boundary of *Mecynocera* for individual CalCOFI cruises from June 1949 to July 1951 off California and Baja California.

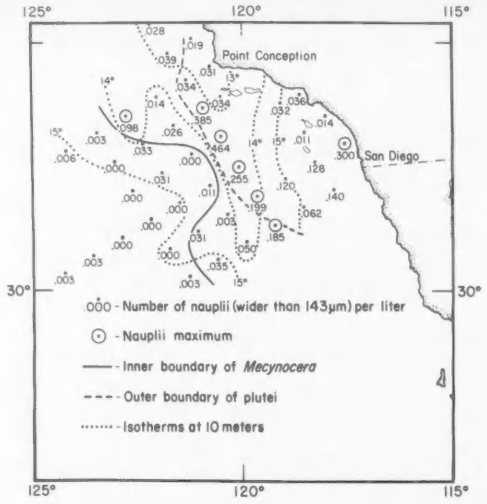

FIGURE 3.—Distribution of copepod nauplii (wider than 143 μm) and their relation to some other biological and physical variables during June 1950.

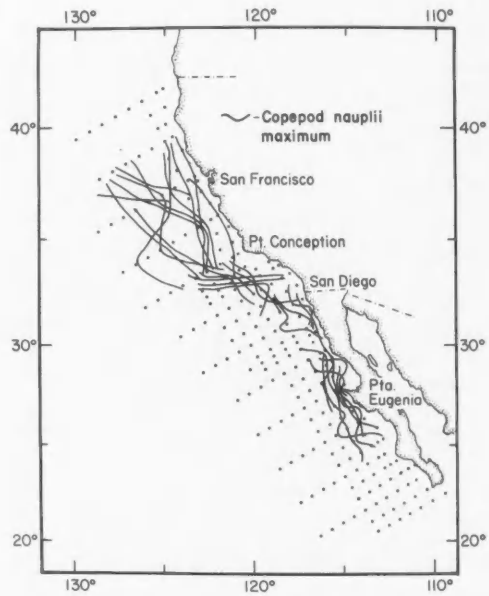

FIGURE 4.—Copepod nauplii maxima for individual CalCOFI cruises from June 1949 to July 1951.

study of plankton off La Jolla, Beers and Stewart (1970), using 35-μm mesh nets, found that for the three stations located 1.4, 4.6, and 12.1 km from shore, naupliar densities averaged 63/liter, 33/liter, and 26/liter, respectively.

The zone of maximum nauplii seems to be associated with the *Mecynocera* boundary, which is also indicated in Figure 3. The station of maximum nauplii for a line usually occurs one to three stations onshore of this boundary.

As may be seen in Figure 3, there appears to be an association between the zone of maximum nauplii and the tongue of relatively cold water (13° and 14° isotherms) extending south of Point Conception. This cold tongue probably is nutrient rich water upwelled north of Point Conception. Shoreward from this zone lies the counterclockwise gyre of the Southern California Bight, extending from Point Conception to northern Baja California. Allen (1939) stated that his most offshore station, located 120 km from the coast, which is in the general vicinity of the nauplii maximum, was consistently the richest station for microcrustacea. Berner (1959) noted that stations where he found anchovy larvae to be feeding were in the area of the copepod nauplii maximum as described by Arthur (1956).

In the San Francisco area, where two maxima are commonly found, the outer one is usually about 115 to 400 km offshore (Figure 4). The maximum zone is consistently found seaward from the Channel Islands, about 100 to 320 km off the mainland shore. Occasionally nauplii-rich stations are found inside the islands. The average nauplii maximum approaches the coast south of San Diego, and is adjacent to the shoreline in northern Baja California, probably a result of upwelling along the coast. From Punta Eugenia south, this zone becomes irregular, as does the *Mecynocera* boundary.

QUANTITATIVE DISTRIBUTION OF MICROCOPEPODIDS AND NAUPLII IN THE CALCOFI AREA

On examining the values obtained in this program, it is apparent that there are very wide ranges in densities. Values for microcopepodids range from 0.003 to 7.886/liter. Nauplii were sampled in numbers ranging from 0 to 17.280/liter. Frequency distributions are highly skewed toward the lower densities. To overcome this problem, the data are presented as logarithms to normalize the frequency distributions.

The method used for comparing data is the ogive, or cumulative frequency curve. The ogive is useful to depict what percentage of the samples from an area contains any particular concentration of copepodids or their nauplii. Furthermore, in considering concentrations of any two areas, the value of the 50 percentile concentrations can be quickly read off and compared. The 50 percentile value in this particular type of distribution lies very near the mode and so may be considered to closely represent the most common value of concentration for a given area.

Ogives for nauplii and microcopepodids as sampled by all Clarke–Bumpus and all microplankton samples in both the onshore zone and offshore zone are presented in Figure 5. Because of the large mesh size of the nets used, most nauplii escaped which resulted in more copepodids than nauplii being caught. The truncated net (56-μm mesh) caught more nauplii than copepodids. Very few samples were taken in the offshore zone with the truncated net and so it cannot be compared with the other two samplers in this manner. Differences in the ratios of onshore zone to offshore zone for the 50 percentile values are as follows:

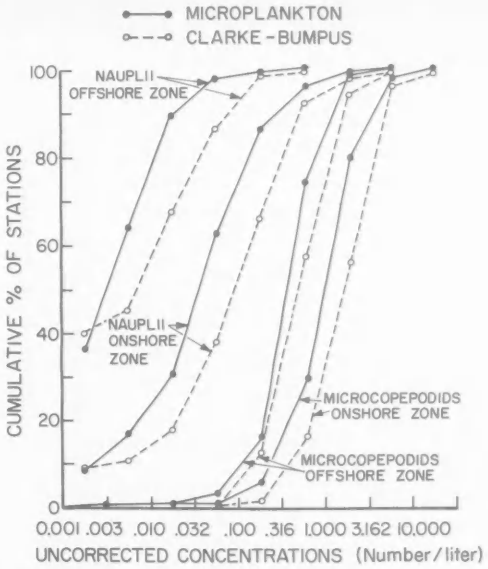

FIGURE 5.—Ogives for abundance of nauplii and microcopepodids in offshore and onshore zones as sampled with the Clarke–Bumpus (120-μm mesh) and microplankton samplers (143-μm mesh).

Sampler	*Microcopepodids*	*Nauplii*
Clarke–Bumpus	3.17:1	12.58:1
Microplankton	2.57:1	11.22:1

There are about two and one-half to three times as many copepodids in the onshore zone as there are in the offshore zone. There are, however, about 12 times as many nauplii in the former as in the latter. There are about four times as many nauplii per copepodid in the onshore zone as in the offshore zone. This is probably a result of the increased fecundity of copepods living in the richer phytoplankton owing to upwelling in the onshore zone.

CORRECTING FOR CALIBRATION ERRORS AND ESCAPEMENT

The ogive was useful to correct errors of the various samplers used in this survey. Figure 6 presents the ogives obtained for microcopepodids by all samples taken in the onshore zone with the three different samplers. Of the three samplers, the Clarke–Bumpus was the most accurately calibrated for volume and so the other two samplers were corrected to it. Such a correction can be made

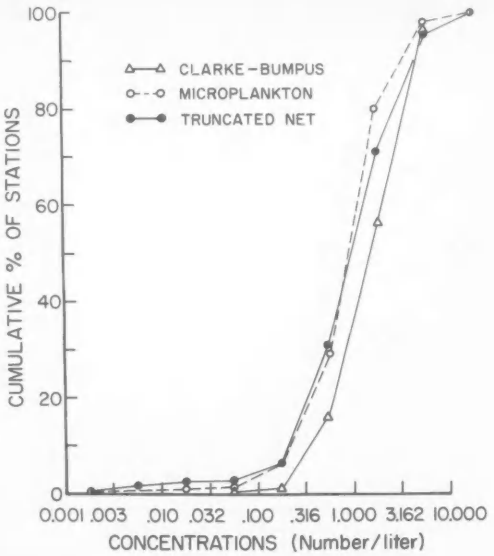

FIGURE 6.—Ogives for abundance of microcopepodids in the onshore zone as sampled by the three samplers.

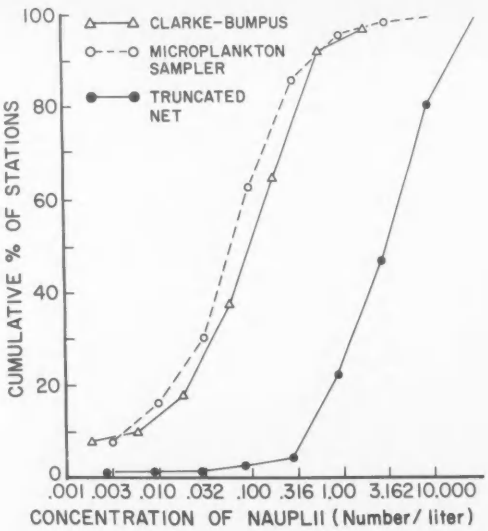

FIGURE 7.—Ogives for nauplii of all sizes retained by each of the three samplers in the onshore zone corrected for volume filtered.

by measuring their 50 percentile differences and adding this value to all the points along their respective curves. This correction assumes that all net meshes used retained copepodids in equal percentages. This is not entirely correct as Beers and Stewart (1967) reported that some copepodids can escape even a 35-μm mesh.

Having corrected the volume errors of the three devices (or, at least, made them comparable in value), we can now roughly correct for the amount of escapement by nauplii through the three different mesh sizes. Figure 7 presents ogives for nauplii in the onshore zone as sampled by the three devices, the numbers of which have been corrected for volume strained by values obtained by the 50 percentile differences in Figure 6. These ogives are based upon the same amount of water filtered, thus their differences are due to differential escapement of nauplii. By comparing the 50 percentile values in Figure 7, the following approximation of the size distribution of the naupliar population in the onshore zone is obtained:

Sampler	*Mesh opening (μm)*	*Usual number retained/liter*
Truncated net	56	2.884
Clarke–Bumpus	120	0.095
Microplankton	143	0.058

A plankton net hauled from some depth to the surface may pass through a wide range of plankton concentrations but its catch will represent only the average of these conditions and will not reveal rich but thin strata that might exist. The above concentrations, therefore, probably underestimate somewhat the highest concentrations found in the usual water column.

When the ogives for the three samplers are corrected to the Clarke–Bumpus for volume and to the truncated net for escapement, by their 50 percentile differences (Figure 8), they are similar over the mid-60% of their ranges. It is interesting that the three curves for nauplii are so similar when it is considered that two of them represent, primarily, the small percentage contributed by larger nauplii. This implies that the various sizes of nauplii have essentially the same type of distribution and with the same degree of patchiness.

The slope of an ogive is determined by the degree of dispersion within the samples. If the distribution of an organism is so homogeneous that all the observations should fall in one interval, then the resultant ogive would be a vertical line. With wider ranges of densities the ogive will slope less abruptly. By comparing slopes of the two sets of ogives in Figure 8, it can be seen that the copepodid stages are more uniformly distributed than are nauplii.

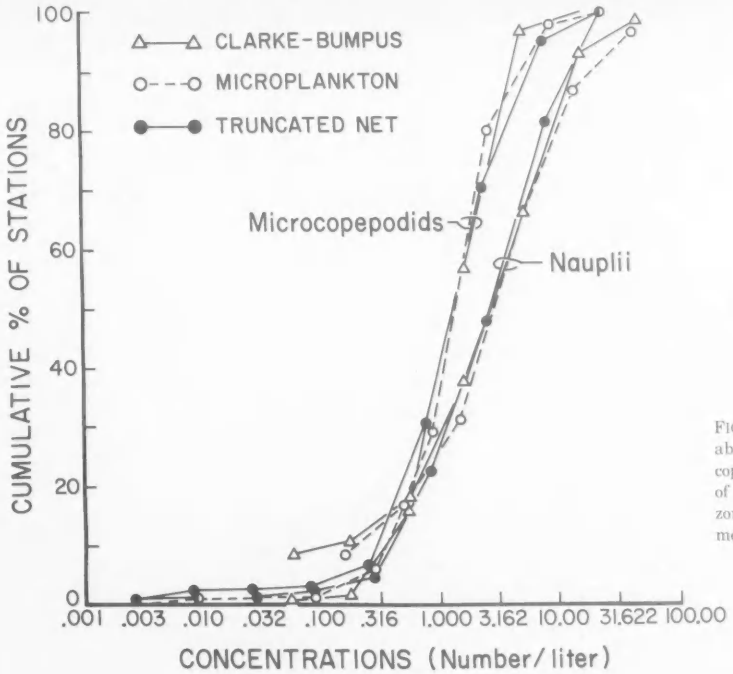

FIGURE 8.—Comparison of ogives for abundance of nauplii and microcopepodids for all sizes retained by each of the three samplers in the onshore zone corrected for volume and escapement.

DISCUSSION

Microcopepod Size and Feeding Habits of Three Larval Fishes

Feeding habits of larvae of Pacific sardine, *Sardinops sagax*; northern anchovy, *Engraulis mordax*; and jack mackerel, *Trachurus symmetricus*, as reported by Arthur (1976), may have been associated with spawning distribution of the adult fish as well as with the distribution of microcopepods and nauplii during the years of this program. Jack mackerel spawned mainly in the offshore zone, as can be determined by comparing the *Mecynocera* boundary with the distribution of jack mackerel larvae (Anonymous 1953:36). Jack mackerel larvae first start to feed when 3.0 mm long and ingest mostly 60- to 70-μm wide (total range 50 to 200 μm) copepod nauplii. However, when they have grown to 3.5 mm their food is primarily about 125-μm wide copepodid stages of small copepod species and when 9.0 mm long they eat 250- to 450-μm wide copepodids of larger species. The quick change from nauplii to copepodids, which is facilitated by their relatively large mouths, may be related to the low nauplii/copepodid ratio of the offshore zone.

Most anchovy larvae were caught inside the *Mecynocera* boundary (Anonymous 1953:34). The more omnivorous 3.0-mm long first feeding anchovy larvae select food from the 25 to 100 μm range with little preference for any size within this range. Food size increases to 125 μm when larvae are about 4.0 mm after which, though there is some increase, food size does not increase isometrically with the increase in length of larvae. This curious slow increase in food size appears to be common to early larval stages of the genus *Engraulis*, as can be observed in food-size/larval-length graphs for Japanese anchovy, *E. japonica* (Yokota et al. 1961), Argentine anchovy, *E. anchoita* (Ciechomski 1967), Peruvian anchovy, *E. ringens* (Rojas de Mendiola 1974), and can be calculated for northern anchovy, *E. mordax*, from data presented by Berner (1959) and Arthur (1976). This lack of selecting for the largest ingestible food size may be related to the high nauplii/copepodid ratio of the inshore zone and may also account for the importance of copepod eggs in the diets of anchovy larvae as reported by the above authors except Yokota et al. (1961).

Sardines spawn near the *Mecynocera* boundary, inshore of the jack mackerel and mostly offshore of anchovy (Anonymous 1953:22), but, also, more southerly of the other two. Sardine larvae combine some feeding characteristics of jack mackerel and anchovy larvae. Food particle size of sardine larvae increases isometrically with length of larvae as in jack mackerel but is smaller for unit larval length and is composed more of copepod eggs and nauplii as in anchovy larvae.

Microcopepod Densities Influence Larval Fish Survival

Other investigations in the CalCOFI area, and in similar latitudes in Japanese waters, helped to approximate the biomass spectrum of the naupliar population. Beers and Stewart (1967) estimated numbers of various microzooplankton at five locations across the California Current. Samples were taken by pumping water through several sizes of filters from depths ranging from the surface to 105 m. Their values for copepod nauplii, averaged and integrated, are compared with the values reported herein as follows:

Mesh size	*Nauplii/ liter*	*Logrithm*	*Source*
Total no., all sizes	22.078	1.3440	Beers and Stewart
Retained by 35 μm	3.878	0.5886	Beers and Stewart
Retained by 56 μm	2.884	0.4600	This report
Retained by 103 μm	0.198	−0.7033	Beers and Stewart
Retained by 120 μm	0.095	−1.0223	This report
Retained by 143 μm	0.058	−1.2366	This report

Logarithms of the above, plotted in Figure 9, are highly correlated with mesh size for the two individual sets of data as well as when they are combined. The line in Figure 9 is a least square fit to all data points combined and is expressed as:

$$N = -0.0188w + 1.3370 \quad \text{(intercept at size 0)} \qquad (1)$$

where N is concentration of nauplii (number per liter) and w is mesh aperture size. The correlation coefficient, r, is 0.9931 and the coefficient of determination, r^2, implies that 98.62% of the variation of naupliar concentrations can be explained by mesh size alone.

Least square fits for the two individual sets of data are as follows:

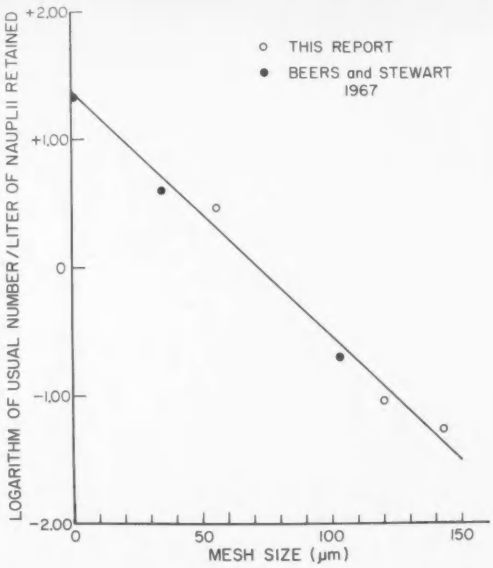

FIGURE 9.—Logarithms of the usual densities of various sizes of nauplii in relation to mesh size. The line is a least square fit to all data points combined from the equation $N = -0.0188w + 1.3370$.

Beers and Stewart

$$N = -0.01976w + 1.31857 \qquad (2)$$
$$r = 0.9994,\ r^2 = 0.9988.$$

This report

$$N = -0.02029w + 1.5577 \qquad (3)$$
$$r = 0.9900,\ r^2 = 0.9801.$$

The microcopepod assemblage in onshore water off the southern California–northern Baja California coast is strikingly similar to that in coastal waters at the same latitudes on the other side of the Pacific. Yokota et al. (1961) measured widths and lengths of 8,839 copepod nauplii and 1,389 copepodids from 666 samples captured in 1-liter containers from an area off the southeast coast of Kyushu over a 2-yr period. Average widths and lengths of nauplii were 67.7 and 156.1 μm, respectively, with a length to width ratio of 2.306. Assuming a cylindrical form, the average Kyushu nauplius has a volume of about 562,000 μm^3 which differs by only about 10% from the 510,000 μm^3 volume of the average La Jolla nauplius (Beers and Stewart 1970). Concentrations ranged from 0 to 524 nauplii/liter (only two samples were greater than 100/liter) with an

average of 13.27/liter. Size distribution as calculated from the data of Yokota et al. (1961) is:

Width of nauplii	*Average number/liter*
All sizes	13.27
>50 μm	3.87
>100 μm	0.53
>150 μm	0.10
>200 μm	0.05

In comparing the Kyushu to the California area it appears that there are fewer very small nauplii but about twice as many larger nauplii. These differences may result from the Kyushu samples being taken at the surface whereas the California samples were collected at varying depths.

Usual densities of total nauplii and copepodids of all sizes calculated from the several investigations discussed herein are as follows:

Nauplii/ liter	*Copepodids/ liter*	*Source*
36.12	1.41	This report, Equation (3)
13.27	2.10	Averaged from Yokota et al. 1961
22.08	36.35	Averaged from Beers and Stewart 1967
34.33	4.17	Averaged from Beers and Stewart 1970

The calculated number of nauplii of all sizes from this report appears to be somewhat high which may result from being derived by extrapolating from Equation (3). The average number of copepodids found by Beers and Stewart (1967) appeared to be much higher than the other investigations and may be a result of sampling an unusually rich but short-lived condition (all samples were taken during a 7-day period). Numbers of nauplii and copepodids of Beers and Stewart (1970) should be somewhat higher than the average for coastal areas because they were taken very close to the beach. In general, the usual densities in onshore areas at these latitudes (30°–35°N) is about 1.5 to 4 copepodids/liter and about 13 to 30 nauplii/liter. These densities are similar to those found by Allen (1939) who, while studying phytoplankton off California by trapping 5-liter samples, found that the combined densities of nauplii and copepodids ranged from 10 to 30/liter. Copepod nauplii average about 20–30/liter in Japanese coastal waters and 10 or less/liter in the warm offshore Kuroshio (Honjo et al.[3,4]).

These densities are considerably lower than those usually reported to be required to support growth of marine teleost larvae in the laboratory as is illustrated by a few examples. O'Connell and Raymond (1970) found poor survival of anchovy larvae in densities of nauplii and copepodids of less than 4,000/liter. Hunter (in press) used 100,000 *Gymnodinum*/liter combined with 8,000 to 115,000 rotifers/liter to grow early anchovy larvae. Houde (1975) found best survival of larval sea bream, *Archosargus rhomboidalis*, was on 50- to 100-μm wide nauplii and copepodids in densities of 1,500–3,000/liter, but 10% survived at 100/liter at low larval stock densities. In coastal and offshore areas even the highest densities of nauplii reported do not equal those used in most laboratory rearing experiments. The highest concentration of larger than 56-μm nauplii I encountered was 17.28/liter which indicates that, calculating from Equation (1), for nauplii of all sizes there were about 195/liter. Highest concentrations reported by others are 524/liter (Yokota et al. 1961), 180/liter (Beers and Stewart 1970), and 134/liter (Allen 1939).

Gallagher and Burdick (1970) calculated that the mean distance $\bar{R}$, between a particle and its nearest neighbor in a random three-dimensional array can be computed from $\bar{R} = 0.553960\rho^{-1/3}$, where ρ is their mean density in space. At concentrations of 25 nauplii/liter the distance from the mouth of a fish larva to the nearest nauplius is on the average about 18.9 mm, whereas at 200 nauplii/liter this distance is 9.5 mm.

Concentrations approaching laboratory requirements are encountered in localized conditions, i.e., Schnack (1974) caught nauplii with a 55-μm net in numbers up to 917/liter in a shallow fjord off the western Baltic. Lasker (1975) found the dinoflagellate, *Gymnodinum splendens*, in the ocean in high enough densities (20,000–40,000/liter) to support life of early laboratory-spawned anchovies. These densities were dependent on stable oceanic conditions which were quickly dispersed by a storm.

The reason for the disparity between the observed naupliar densities in the ocean and the

[3]Honjo, K., T. Kidechi, and H. Suzuki. 1959. On the food distribution and survival of post larval iwashi-I-Distribution of food organisms, the food of the anchovy and ecologically related species along the southwestern Pacific coast of Honshu, Sept.–Nov. 1958. Reports on the major coastal fish investigations, and the investigations for forecasting of oceanographic conditions and fisheries (Preliminary Report), February 1959, 7 p. Engl. transl. by S. Hayashi.

[4]Honjo, K., T. Kitachi, and M. Kudo. 1957. Food of the post-larvae of iwashi. Reports of the major coastal fish investigations for 1956 (Preliminary Report) November 1957, 5 p. Engl. transl. by S. Hayashi.

densities required for larval survival in the laboratory may be that present microplankton sampling techniques do not detect small but dense aggregations of nauplii which, however, can be found by fish larvae. It, also, may be that present rearing techniques do not approximate oceanic conditions sufficiently to permit assaying of actual prey concentrations required to allow significant larval survival. Blaxter (1965) reported that the condition factor of herring larvae living in the ocean is worse than that of larvae which died presumably of starvation in the laboratory. This may attest to greater ability of larvae to survive poor rations in the usual oceanic environment than in the laboratory.

Maximum of Naupliar Biomass Spectrum

The abundance of copepod nauplii decreases exponentially with increasing size of individuals (Figure 9), whereas the volume of an individual nauplius increases exponentially with increasing size (roughly by the cube of width). When the naupliar size range is divided into 10-μm wide size classes and the average volume per nauplius is multiplied by numbers of individuals per class (calculated from the equation for combined data, Figure 9) it is seen that the naupliar biomass is at a maximum at about the 70 μm width (Figure 10) even though there are many more nauplii of smaller sizes.

Figure 10 includes, also, the food-particle size range at first feeding of larvae of Pacific sardine, northern anchovy, and jack mackerel (Arthur 1976). It is interesting to note that these ranges overlap at the 50- to 80-μm width range which brackets the naupliar biomass spectrum maximum. This suggests that larval feeding habits of these three fishes have evolved to take advantage of this important food resource at first feeding.

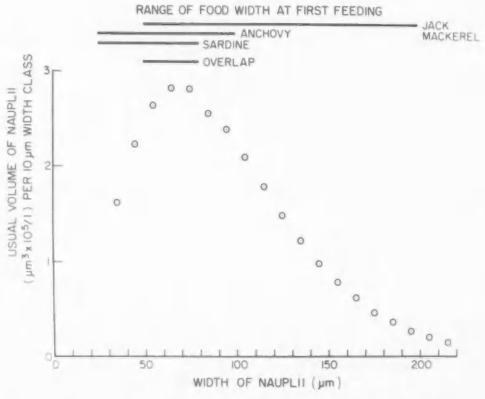

FIGURE 10.—Biomass spectrum of naupliar size range compared with food size at first feeding of the larvae of three fishes in the California Current system.

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ABUNDANCE AND POTENTIAL YIELD OF THE SCALED SARDINE, *HARENGULA JAGUANA*, AND ASPECTS OF ITS EARLY LIFE HISTORY IN THE EASTERN GULF OF MEXICO[1]

EDWARD D. HOUDE[2]

ABSTRACT

Eggs and larvae of the scaled sardine, *Harengula jaguana*, were collected in 1971–74 from the eastern Gulf of Mexico to determine spawning seasons, spawning areas, adult biomass, and fisheries potential. Aspects of the early life history of the species also were studied. Spawning occurred from January to September, but was most intense from May to August, when surface temperatures ranged from 20.8° to 30.7°C and surface salinities were 29.9 to 36.9‰. All spawning occurred between the coast and the 30-m depth contour, mostly within 50 km of the coast. The biomass of scaled sardines, based on annual spawning estimates, apparently increased from 1971 to 1973, the mean estimate for the 3 yr being 184,527 metric tons. Potential yield estimates, based on the 3-yr mean biomass, ranged from 46,000 to 92,000 metric tons. Larval abundance and mortality rates were estimated from 1973 data. More than 99.9% mortality occurred between time of spawning and attainment of 15.5 mm standard length at 20 days of age. Comparisons were made of scaled sardine distribution, abundance, potential yield, and larval mortality with those of other eastern Gulf clupeids.

Scaled sardine, *Harengula jaguana* Poey, is abundant in coastal waters of the western Atlantic from New Jersey to Santos, Brazil, including the Gulf of Mexico (Berry 1964). It is common from Florida to Brazil (Rivas 1963), but there are no large-scale directed fisheries for the species. Klima (1971) reported it to be an abundant, surface-schooling species that is usually found within the 20-fathom curve in the northeastern Gulf of Mexico. It is one of the most common species in Gulf Coast estuaries (Gunter 1945; Springer and Woodburn 1960; Roessler 1970). Because of its abundance, it is an important latent fishery resource in the Gulf of Mexico and Caribbean region (Reintjes and June 1961; Bullis and Thompson 1970; Klima 1971). Small catches of *Harengula* spp. totalling 2,189 metric tons in 1974 presently are landed by Cuba, Brazil, and the Dominican Republic (Food and Agriculture Organization 1975). No reported catches are made by the United States, but a small amount, probably less than 500 tons annually, is landed in Florida for bait in commecial and recreational fishing.

Some aspects of the biology of scaled sardines are known. Low (1973) discussed the species and its occurrence in Biscayne Bay, Fla., including food habits and juvenile growth rates. Fecundity, size at maturity, and spawning were reported by Martinez and Houde (1975). Roessler (1970) discussed growth, recruitment, and the relationship of environmental factors to scaled sardine abundance in an Everglades estuary, and Springer and Woodburn (1960) discussed its ecology in Tampa Bay. Eggs and larvae have been described by Matsuura (1972), Houde and Fore (1973), Houde et al. (1974), and Gorbunova and Zvyagina (1975).

Objectives of this study were to estimate scaled sardine biomass and fishery potential in the eastern Gulf of Mexico from the distribution and abundance of its eggs and larvae. Information on the early life history also was obtained. Similar studies on round herring, *Etrumeus teres*, and thread herring, *Opisthonema oglinum*, were recently published (Houde 1976, 1977a, b).

METHODS

Methods to determine scaled sardine biomass and fisheries potential are the same as those used for round herring and thread herring (Houde 1977a, b). Collecting methods were described (Houde 1977a), and summarized station data from

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the 17 ichthyoplankton cruises have been published (Houde and Chitty 1976; Houde et al. 1976). The survey area and its potential sampling stations were illustrated in figure 1 of Houde (1977a, b). Analytical and statistical procedures are based on those discussed by Saville (1964), Ahlstrom (1968), and Smith and Richardson (in press).

RESULTS AND DISCUSSION

Occurrence of Eggs and Larvae

A total of 19,183 scaled sardine eggs and 3,828 larvae were collected during the 17 cruises, in which 867 stations were sampled. Scaled sardines composed 59.8% of all clupeid eggs collected and their larvae composed 13.2% of all clupeid larvae. Scaled sardine eggs made up 6.3% of the total fish eggs from the 867 stations and their larvae constituted 2.7% of the total larval fish catch.

Scaled sardine eggs or larvae were collected on cruises from January through September, but they were most abundant from May through August (Table 1). Stations where they occurred are given in Figure 1. Distribution and abundance of eggs and larvae are illustrated for the May through August cruises (Figures 2–5). Spawning from January to March probably is confined to the southernmost parts of the survey area, since eggs and larvae were collected only at stations south of lat. 26°N on cruises during those months. No eggs were collected where depths exceeded 30 m (Figure 1). Larval distributions were similar to those for eggs, except for a single anomalous occurrence of larvae at a station on the 200-m depth contour (Figures 1, 3). On cruises CL7405 and CL7412 several stations nearer to shore (of only 4–10 m depth) than any on previous cruises were sampled (Figure 5). On cruise CL7412, when intense spawning was taking place, catches of eggs at the nearshore stations exceeded catches at the regular stations. Mean egg abundance under 10 m² at positive stations was 1.85 times greater at the nearshore stations than at the regular stations (158.93 compared with 85.75). Log_{10} transformed means were tested in a t-test.

Stations	*No. of stations with scaled sardine eggs*	*Log_{10} mean*	*Log_{10} $S_{\bar{x}}$*
Regular	9	1.0056	0.3343
Nearshore	11	1.8118	0.1913

$t_{calc} = 2.15^*$ $\quad t_{0.05(2)18} = 2.10$

Differences were significant ($P<0.05$). Failure to sample nearshore stations on earlier cruises probably resulted in an underestimate of scaled sardine spawning and also an underestimate of adult biomass if egg distribution during cruise CL7412 was representative of earlier cruises.

The observed egg and larvae distributions indicate that most adults are located where depth

TABLE 1.—Summarized data on cruises to the eastern Gulf of Mexico, 1971–74, to estimate abundance of scaled sardine eggs and larvae. GE = RV *Gerda*, 8C = RV *Dan Braman*, TI = RV *Tursiops*, 8B = RV *Bellows*, IS = RV *Columbus Iselin*, *CL* = RV *Calanus*.

Cruise	Dates	Number of stations	Positive stations for eggs[1]	Positive stations for larvae[2]	Mean egg abundance under 10 m²		Mean larvae abundance under 10 m²	
					All stations	Positive stations	All stations	Positive stations
GE7101[3]	1–8 Feb. 1971	20	1	0	0.64	23.05	0.00	0.00
8C7113								
TI7114	7–18 May 1971	123	2	12	0.78	64.66	6.73	51.52
GE7117	26 June–4 July 1971	27	2	0	1.67	19.95	0.00	0.00
8C7120								
TI7121	7–25 Aug. 1971	146	8	8	0.83	28.09	0.21	4.37
TI7131								
8B7132								
GE7127	7–16 Nov. 1971	66	0	0	0.00	—	0.00	—
8B7201								
GE7202	1–11 Feb. 1972	30	0	0	0.00	—	0.00	—
GE7208	1–10 May 1972	30	1	4	1.68	76.21	1.24	11.57
GE7210	12–18 June 1972	13	3	3	35.31	146.94	5.97	22.78
IS7205	9–17 Sept. 1972	34	0	2	0.00	—	0.16	4.70
IS7209	8–16 Nov. 1972	50	0	0	0.00	—	0.00	—
IS7303	19–27 Jan. 1973	51	0	1	0.00	—	0.01	0.26
IS7308	9–17 May 1973	49	8	14	14.38	154.16	9.26	38.34
IS7311	27 June–6 July 1973	51	8	6	31.59	174.14	0.59	5.51
IS7313	3–13 Aug. 1973	50	9	11	67.49	747.09	10.86	50.26
IS7320	6–14 Nov. 1973	51	0	0	0.00	—	0.00	—
CL7405	28 Feb.–9 Mar. 1974	36	0	4	0.00	—	0.39	4.06
CL7412	1–9 May 1974	44	20	23	50.29	125.82	14.45	28.79

[1]Positive station is a station at which scaled sardine eggs were collected.
[2]Positive station is a station at which scaled sardine larvae were collected.
[3]An ICITA 1-m plankton net was used on this cruise. On all other cruises a 61-cm bongo net was used.

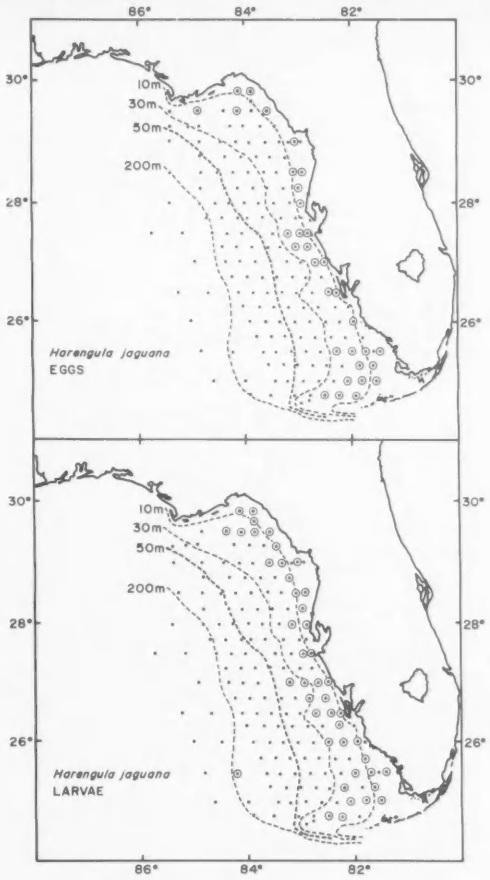

FIGURE 1.—Top. Stations in the survey area where eggs of scaled sardines were collected at least once during 1971–74. Stations where eggs did not occur are indicated by dots. Bottom. Stations in the survey area where larvae of scaled sardines were collected at least once during 1971–74. Stations where larvae did not occur are indicated by dots.

is <20 m and that nearly all are found within the 30-m depth contour. Spawning adults are confined to a band within 85 km of the coast. Klima (1971) reported that scaled sardines in the Gulf of Mexico usually are found within the 20-fathom curve (36.5 m), but he noted occasional occurrence over depths as great as 165 fathoms (302 m). Brazilian scaled sardines also spawned near the coast, within 18.5 km of shore where water depth was <65 m (Matsuura 1972).

There were no areas in the eastern Gulf where consistently high egg or larval catches occurred that would suggest great concentrations of adults. Consistent catches of eggs and larvae between lat. 24°45′N to 25°45′N and long. 81°30′W to 82°30′W, as well as just north of Tampa Bay between lat. 28°00′N to 28°30′N and long. 82°45′W to 83°15′W did indicate that scaled sardines usually were abundant in those areas.

Mean egg abundances for the 17 cruises ranged from 0.00 to 67.49 under 10 m² of sea surface (Table 1). Considering only positive stations, means ranged from 19.95 to 747.09 under 10 m² (Table 1). Abundances of eggs at stations rarely exceeded 100 under 10 m² of sea surface during 1971 and 1972, but frequently were between 100 and 1,000 under 10 m² during 1973 and 1974 (Figures 2–5). Only once, in August 1973, did abundance of eggs exceed 1,000 under 10 m² (Figure 4).

Cruise means for scaled sardine larval abundances ranged from 0.00 to 14.45 under 10 m² when all stations were considered, and from 0.26 to 51.52 under 10 m² at positive stations (Table 1). At positive stations larval abundances usually ranged from 11 to 100 under 10 m², and exceeded 100 under 10 m² at only eight stations during 1971–74 (Figures 2–5).

Most scaled sardine eggs and larvae were found nearer to shore than those of either thread herring or round herring (Houde 1977a, b). However, there was considerable overlap in areas and seasons of occurrence of thread herring and scaled sardine spawning. Eggs and larvae of scaled sardines and round herring did not occur together because round herring did not spawn in water shallower than 30 m, and most spawning by that species occurred during winter.

Temperature and Salinity Relations

Scaled sardine eggs were collected at surface temperatures from 20.8° to 30.7°C and at surface salinities from 29.92 to 36.88‰. Larvae ≤5 mm standard length (SL), 5 days or less in age, were taken at surface temperatures from 18.4° to 30.5°C and surface salinities of 27.27 to 36.88‰. Vertical sections showing temperature and salinity profiles for cruises during the scaled sardine spawning season indicated that surface temperatures differed from those at 10 m by a maximum of only 1°C, but that a maximum difference of 4°C could occur at 30 m. The difference between the surface and the 30-m depth usually did not exceed 2°C. Salinity differences between the surface and 10 m were always <0.5‰ and never exceeded 1.5‰

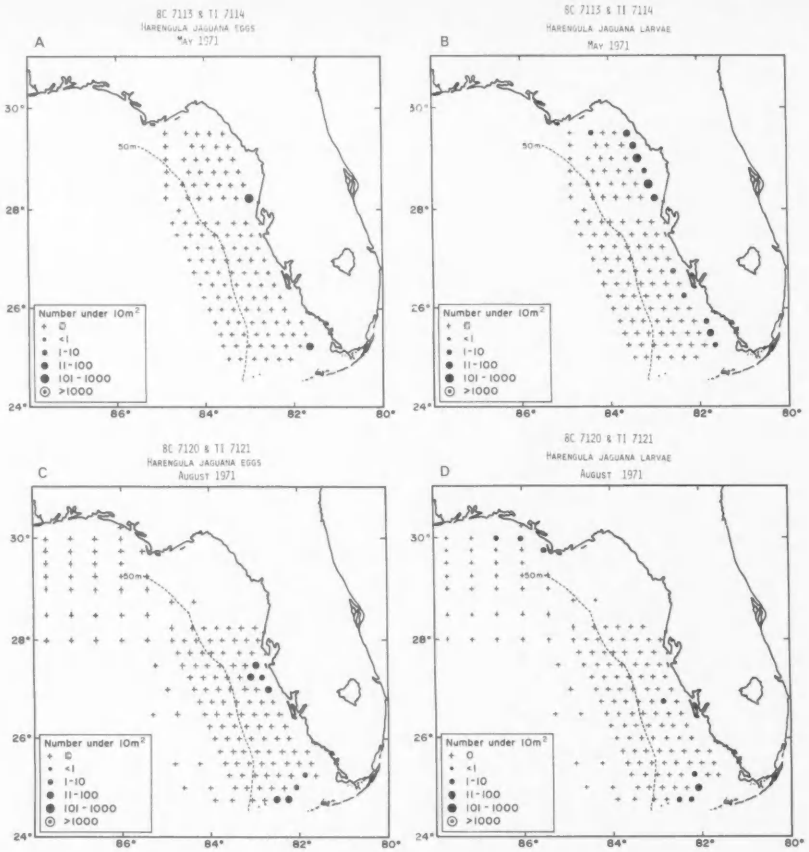

FIGURE 2.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise 8C7113–TI7114, May 1971. C, D. Cruise 8C7120–TI7121, August 1971.

between the surface and 30 m. The buoyant eggs and pelagic larvae probably developed at temperatures and salinities similar to those at the sea surface.

Relatively few eggs or ≤5.0-mm larvae occurred where surface temperature was <24.0°C over the 1971–74 period (Figure 6). For eggs, 82.3% of the station occurrences were at surface temperatures above 24°C; for larvae, 71.0% occurred above 24°C. Although spawning occurred over a wide salinity range, 71.0% of the stations with eggs had salinities that exceeded 35.0‰; 62.3% of the stations with ≤5.0-mm larvae had salinities above 35.0‰.

Matsuura (1972) collected eggs and larvae of Brazilian scaled sardine at temperatures and salinities within the ranges observed for eggs and larvae in the eastern Gulf. Spawning occurred at temperatures and salinities similar to those recorded for thread herring (Houde 1977b). Scaled sardine eggs and larvae were found over slightly wider ranges of temperature and salinity than were thread herring, reflecting the slightly longer spawning season of scaled sardines in the eastern Gulf and their tendency to be most abundant nearer to the coast where temperatures and salinities varied most.

Egg and Larval Abundance in Relation to Zooplankton

There was no apparent relationship between either egg or larval abundance at stations and

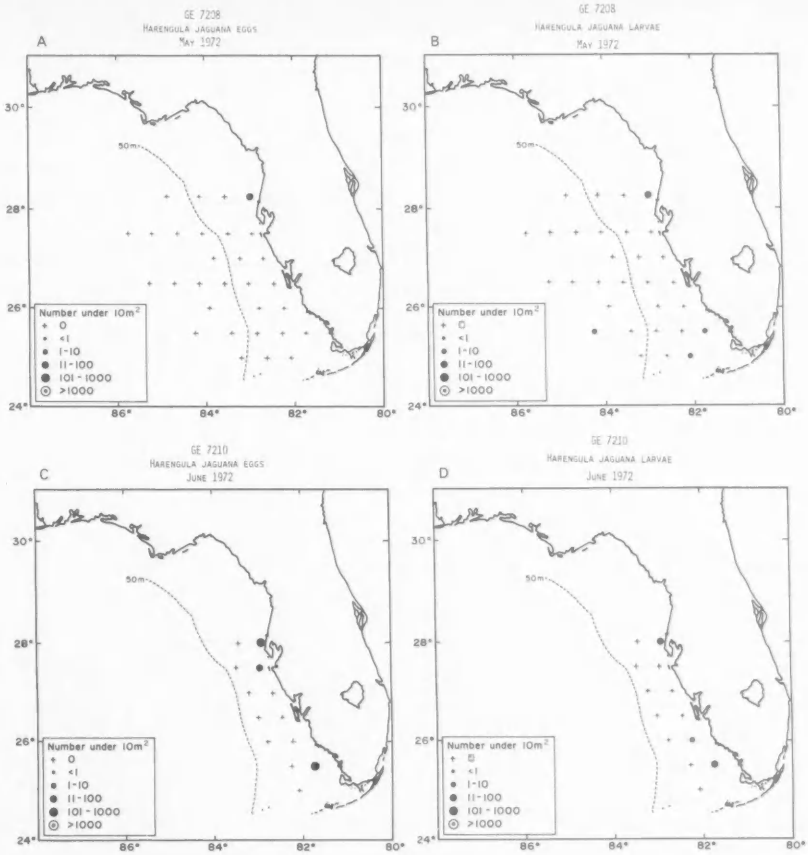

FIGURE 3.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise GE7208, May 1972. C, D. Cruise GE7210, June 1972.

volume of zooplankton collected in the 333-μm mesh bongo net in 1972–74. Mean zooplankton volume was 153.4 cm³/1,000 m³ in 1972–74 (Houde and Chitty 1976). Highest abundances of scaled sardine eggs and larvae occurred where zooplankton volumes exceeded 153.4 cm³/1,000 m³ but correlations between zooplankton volume and scaled sardine egg or larval abundance were not significant. Because the 333-μm mesh did not collect small copepod nauplii, a major food of fish larvae, and because zooplankton was not identified, significant correlations between larvae and zooplankton were unlikely. The relatively high catches of eggs at stations with high zooplankton volumes may have reflected the ability of scaled sardine adults to concentrate in rich zooplankton areas, rather than indicating that eggs were spawned where food would be abundant for larvae.

Relative Fecundity and Size at Maturity

Mean relative fecundity of scaled sardines is 528.0 ova/g ($S_{\bar{x}}$ = 26.5 ova/g), based on data from 22 females collected near Miami, Fla., by Martinez and Houde (1975). They found that two modal groups of ova ripened during the spawning season and that both modes apparently were spawned. The relative fecundity estimate here differs slightly from their reported value because they estimated it for female weights minus ovary weights. To determine stock biomass, the best

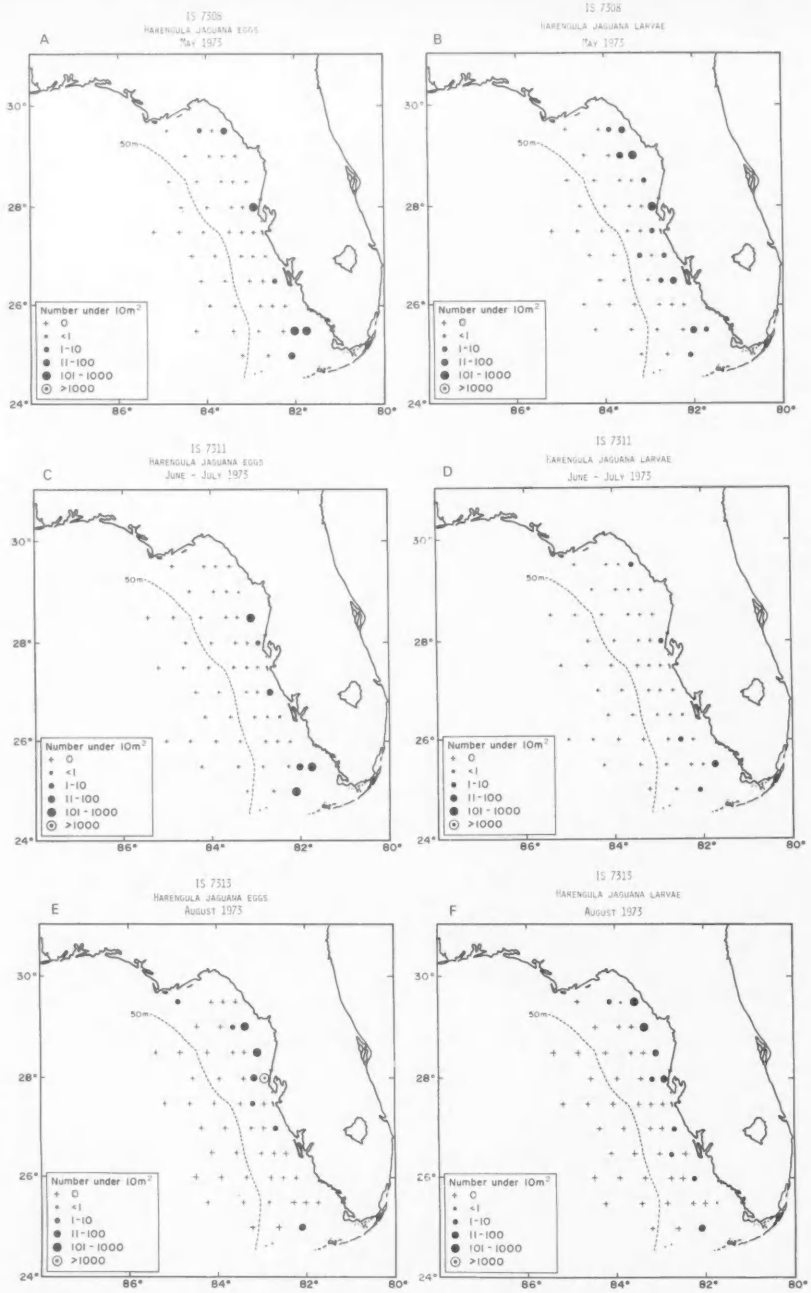

FIGURE 4.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m^2 of sea surface. A, B. Cruise IS7308, May 1973. C, D. Cruise IS7311, June–July 1973. E, F. Cruise IS7313, August 1973.

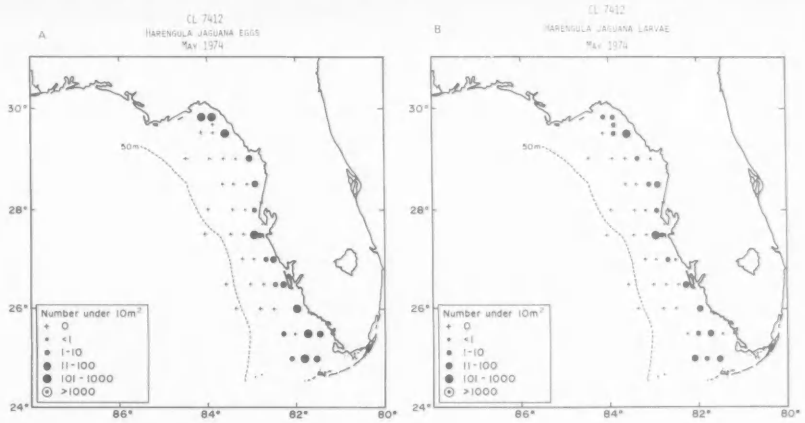

FIGURE 5.—Distribution and abundance of scaled sardine eggs and larvae. Catches are standardized to numbers under 10 m² of sea surface. A, B. Cruise CL7412, May 1974.

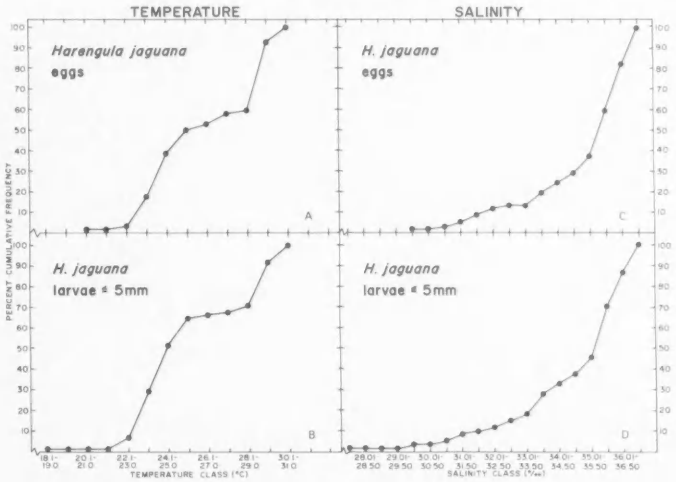

FIGURE 6.—Percent cumulative frequency distribution of 1971–74 stations where scaled sardine eggs occurred in relation to surface temperatures (A) and to surface salinities (C), and ≤5.0-mm SL larvae occurred in relation to surface temperatures (B) and surface salinities (D).

relative fecundity estimate is for total weight, including ovary and the estimate given here is based on that criterion. Because relative fecundity did not differ significantly among females from 8.5 to 16.3 cm SL (14.8 to 98.4 g) (Martinez and Houde 1975), the mean value was used in calculating biomass estimates. Mean relative fecundity with 0.95 confidence limits is 528.0 ± 55.1 ova/g. It seems unlikely that biomass estimating errors greater than ±10% could be attributable to errors in fecundity estimates.

Cruise Egg Abundance

The estimated abundances of scaled sardine eggs, before correction for egg stage duration, within the areas represented by each of the cruises range from 0.00 to 103.39 × 10^{10} (Table 2). The Table 2 estimates, which represent the number of eggs present on a day during a cruise, were corrected for egg stage duration and then expanded to represent the number of days encompassed by the cruise period (Sette and Ahlstrom 1948; Houde 1977a), before they were used in the biomass estimating procedure.

Time Until Hatching

Egg stage duration is less than 24 h for scaled sardines when temperatures are above 24°C.

TABLE 2.—Abundance estimates of scaled sardine eggs for each cruise. Estimates were obtained using equations (2) and (3) (Houde 1977a) and are not corrected for duration of the egg stage.

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise egg abundance (eggs $\times 10^{10}$)
GE7101	25.79	0.77	0.18
8C7113 and TI7114	120.48	18.32	0.94
GE7117	101.10	7.93	1.69
8C7120 and TI7121	189.43	13.41	1.57
GE7127, 8B7132 and TI7131	72.99	0.00	0.00
8B7201 and GE7202	148.85	0.00	0.00
GE7208	124.88	27.56	2.51
GE7210	48.43	15.60	17.10
IS7205	104.59	4.88	0.00
IS7209	149.80	0.00	0.00
IS7303	149.80	3.05	0.00
IS7308	151.42	43.38	21.77
IS7311	156.50	25.43	49.44
IS7313	153.18	40.79	103.39
IS7320	153.89	0.00	0.00
CL7405	52.00	5.84	0.00
CL7412	91.33	43.45	45.93

[1]Positive area is defined as the area representing stations where either eggs or larvae of scaled sardines were collected.

Newly fertilized eggs were collected only at night in the Gulf of Mexico surveys and only advanced embryos usually were present from midday to late afternoon. Similar observations were made for scaled sardine eggs collected near Miami and used in laboratory rearing experiments (Houde and Palko 1970; Houde et al. 1974). The estimated peak spawning time is 2200 h.

Egg abundance was underestimated on most cruises because hatching time was less than 1 day. All cruise abundances were adjusted by dividing them by the estimated mean egg stage duration (Table 3) before annual spawning estimates were made.

Adjusting Cruise Egg Abundance Estimates for Area

Some cruises did not completely cover the area within the 30-m depth contour of the eastern Gulf where scaled sardines spawned. Egg abundance estimates for those cruises were adjusted by dividing the cruise abundance estimate (Table 2) by an adjustment factor, the proportion of the spawning area represented by the cruise. Egg abundance estimates were adjusted for cruises GE7117, 8C7120–TI7121, GE7208, and GE7210. Area adjustment factors were: GE7117—0.394; 8C7120–TI7121—0.746; GE7208—0.644; and GE7210—0.574. Cruise IS7205, in which scaled sardine larvae but no eggs were taken, also did not encompass the entire spawning area. Larval abundance estimates were adjusted for that cruise by its area factor, 0.750. Cruise egg abundance estimates from Table 2, after adjustment, were: GE7117—4.29×10^{10}; 8C7120–TI7121—2.10×10^{10}; GE7208—3.90×10^{10}; and GE7210—29.79×10^{10}.

TABLE 3.—Assigned egg stage durations of scaled sardine eggs for each cruise in which they occurred, 1971–73.

Cruise	Egg stage duration (days)	Cruise	Egg stage duration (days)
GE7101	1.17	GE7208	0.84
8C7113		GE7210	0.80
TI7114	0.84	IS7308	0.84
GE7117	0.80	IS7311	0.80
8C7120		IS7313	0.80
TI7121	0.80		

Annual Spawning and Biomass Estimates

Method I

Estimates of total annual spawning by scaled sardines were obtained after egg stage duration and area factor corrections had been made on daily spawning estimates using the Sette and Ahlstrom (1948) method and procedures described by Houde (1977a). They were: 44.106×10^{11} eggs in 1971, 391.357×10^{11} eggs in 1972, and $1{,}025.834 \times 10^{11}$ eggs in 1973 (Table 4). No estimate was obtained in 1974 because the entire season was not surveyed, but the abundance of eggs from cruise CL7412 (Table 2) suggested that annual spawning was high in that year.

Estimated biomasses increased from 16,708 metric tons in 1971 to 148,255 metric tons in 1972, and to 388,610 metric tons in 1973 (Table 4). Variance estimates for each year's spawning (Table 4) were used to place 0.95 confidence intervals on biomass estimates. These ranged from 0 to 56,210 metric tons in 1971, 0 to 327,130 metric tons in 1972, and 300,965 to 476,271 metric tons in 1973. The mean of the three annual biomass estimates was 184,527 metric tons. The 1972 estimate may be unreliable because of poor area coverage and curtailment of cruise GE7210 due to a hurricane, but the low 1971 estimate probably is accurate because area coverage was good on cruises during the peak spawning period.

A severe red tide in 1971 occurred during spring and summer along the Florida coast of the Gulf of Mexico (Steidinger and Ingle 1972), and it may have caused a high mortality of adult scaled sardines. Dead scaled sardines were observed in red tide areas during cruise GE7117. It is also possible

TABLE 4.—Annual spawning and biomass estimates for scaled sardines from the eastern Gulf of Mexico during 1971, 1972, and 1973 spawning seasons. Estimates are based on the Sette and Ahlstrom (1948) technique. Details of the estimating procedure are given in Houde (1977a).

Year	Cruise	Daily spawning estimate (eggs $\times 10^{11}$)	Days represented by cruise	Eggs spawned during cruise period ($\times 10^{11}$)	Variance estimates on spawned eggs ($\times 10^{24}$)	Adult biomass (metric tons)
1971	GE7101	0.015	51.5	0.773	0.134	
	8C7113					
	TI7114	0.112	74.5	8.344	1.950	
	GE7117	0.541	44.5	24.074	22.959	
	8C7120					
	TI7121	0.263	41.5	10.915	2.121	
Annual total				44.106	27.164	16,708
1972	8B7201					
	GE7202	0.000	50.0	0.000	—	
	GE7208	0.468	65.0	30.420	22.664	
	GE7210	3.721	97.0	360.937	534.743	
Annual total				391.357	557.407	148,255
1973	IS7303	0.000	63.5	0.000	—	
	IS7308	2.613	79.5	207.734	56.388	
	IS7311	6.180	43.5	268.830	42.829	
	IS7313	12.924	42.5	549.270	34.628	
Annual total				1,025.834	133.845	388,610

that few adult scaled sardines were killed, but that they did not spawn during red tides or that spawned eggs experienced high mortality. Failure to spawn or unusual egg mortality could have caused biomass to be underestimated in that year.

Effects on biomass estimates of area adjustments for the four cruises that did not completely cover the scaled sardine spawning area were important. Unadjusted biomass in 1971 was only 10,100 metric tons, 60.5% of the adjusted estimate; in 1972 it was 85,964 metric tons, 58.0% of the adjusted estimate.

Method II

Biomass estimates, using Simpson's (1959) method in a modified form (Houde 1977a), were calculated (Table 5). Mean biomass estimated for the 3 yr was 146,595 metric tons.

TABLE 5.—Annual spawning and biomass estimates for scaled sardines from the eastern Gulf of Mexico during 1971, 1972, and 1973. Estimates are based on the method described by Simpson (1959).

Year	Cruise	Daily spawning estimate (eggs $\times 10^{11}$)	Annual spawning estimate (eggs $\times 10^{11}$)	Adult biomass (metric tons)
1971	GE7101	0.015		
	8C7113			
	TI7114	0.112		
	GE7117	0.541		
	8C7120			
	TI7121	0.263		
			42.981	16,282
1972	8B7201			
	GE7202	0.000		
	GE7208	0.468		
	GE7210	3.721		
			245.940	93,168
1973	IS7303	0.000		
	IS7308	2.613		
	IS7311	6.180		
	IS7313	12.924		
			872.000	330,334

Most Probable Biomass

Scaled sardines as small as 8.0 cm SL are mature (Martinez and Houde 1975), and estimates of adult biomass from egg and larvae surveys probably include most of the stock, juvenile weights being relatively insignificant. Biomass estimates ranged from 16,000 to nearly 400,000 metric tons and stock apparently increased from 1971 to 1973. The evidence from cruise CL7412 indicated that spawning increased nearer to shore than measured at regular survey stations. This suggests that biomasses were underestimated, perhaps by as much as 30%. If so, then biomass may have ranged from 23,000 to 571,000 metric tons during 1971–73, the mean being 265,000 metric tons. Despite variability in estimates, it is clear that the eastern Gulf scaled sardine stock was less than 700,000 metric tons between 1971 and 1973, and it apparently was less than 100,000 metric tons in 1971.

Comparison of Scaled Sardine Biomass With That of Other Clupeids

Biomass of scaled sardines in the eastern Gulf of Mexico is similar to that reported for round herring and thread herring (Houde 1977a, b). Mean biomass of round herring was estimated to be approximately 400,000 metric tons, mostly distributed between the 30- and 200-m depth contours, while thread herring mean biomass was about 250,000 metric tons, much of it occurring in the same areas as scaled sardine, although

many thread herring also occurred farther offshore (Houde 1977b). In aggregate the three species totalled approximately 850,000 metric tons. The menhaden (*Brevoortia* spp.) resource apparently is small in the survey area, since relatively few eggs and larvae were collected (Houde et al. 1976). No estimate of Spanish sardine (*Sardinella* spp.) biomass was obtained, but its eggs and larvae were abundant (Houde et al. 1976). Its biomass may be as great as that for thread herring, i.e., 250,000 metric tons. If true, then aggregate adult biomass of unfished clupeids exceeds 1 million metric tons. The contention that large potential fisheries exist in the eastern Gulf of Mexico is supported by the estimated biomasses. However, none of the individual species appears to represent a resource as large as that of Gulf menhaden, *B. patronus*, which presently yields about 500,000 metric tons annually to the northern Gulf fishery.

Concentration of Biomass

Scaled sardine eggs and larvae occurred in most of the 76 $\times$ 10^9 m^2 area between the coast and 30-m depth contour, except for approximately 15 to 20 $\times$ 10^9 m^2 in the northeastern part of the survey area (Figure 1). During the spawning season, adult scaled sardines were assumed to occur in 60 $\times$ 10^9 m^2 of the eastern Gulf. Concentration of biomass, assuming an even distribution, based on the annual biomass estimates from Method I (Table 4) and their 0.95 confidence limits were: 1971, 0 to 9.4 kg/ha; 1972, 0 to 54.5 kg/ha; and 1973, 50.2 to 79.4 kg/ha. Mean biomass concentrations were: 1971, 2.8 kg/ha; 1972, 24.7 kg/ha; and 1973, 64.8 kg/ha. Estimated scaled sardine biomasses under a hectare of sea surface are similar to those of thread herring but less than those of round herring (Houde 1977a, b).

Potential Yield to a Fishery

Estimates of annual yield varied greatly from year to year, reflecting the biomass fluctuations (Table 6). The estimator $C_{max} = XMB_0$ was used to predict potential maximum sustainable yield (Alverson and Pereyra 1969; Gulland 1971, 1972). X is assumed to equal 0.5 and B_0 is the virgin biomass. M, the natural mortality coefficient, was allowed to vary from 0.5 to 1.0, values that are probable for scaled sardines. The range of potential yields over the 3-yr period was 4,177 to 194,305 metric tons (Table 6). Based on mean biomass estimates for 1971–73, potential yield was between 46,132 and 92,264 metric tons. If scaled sardines were evenly distributed over the 60 $\times$ 10^9 m^2 where they occur in the eastern Gulf, harvestable annual yield, based on 1971–73 mean biomass, is 7.7 to 15.4 kg/ha.

TABLE 6.—Range of potential yield estimates for eastern Gulf of Mexico scaled sardines, based on biomass estimates in 1971, 1972, and 1973 by the Sette and Ahlstrom (1948) method. Yields are predicted at three possible values of M, the natural mortality coefficient. Biomass estimates were obtained from values in Table 4.

Year	Biomass estimate (metric tons)	Estimated potential annual yields (metric tons) for given values of M		
		M=0.50	M=0.75	M=1.0
1971	16,708	4,177	6,266	8,354
1972	148,255	37,064	55,596	74,128
1973	388,610	97,153	145,729	194,305
Mean of 3 yr	184,527	46,132	69,198	92,264

Comparison of Potential Yield With That of Other Clupeids

Potential yield of scaled sardines is slightly less than that estimated for thread herring and less than that for round herring (Houde 1977a, b). Using mean annual biomass estimates by Method I, and the value 1.0 for M, potential maximum sustainable yields are: scaled sardines—92,264 metric tons; thread herring—120,598 metric tons; and round herring—212,238 metric tons. Total potential for the three species is 425,100 metric tons. If Spanish sardines are as abundant as thread herring, they could contribute another 120,000 metric tons raising the aggregate potential yield to 545,100 metric tons.

Potential yields were estimated for adult stock. If a significant biomass of harvestable juveniles is present, they could contribute to the yield. For scaled sardines, and probably round herring (Houde 1977a), small size at first maturity makes it unlikely that a significant, unestimated juvenile biomass is present, but the large size at first maturity of thread herring (Prest[3]) and Spanish sardines (Varea Rivero 1967) indicates that a significant unestimated biomass of juveniles may be present.

[3]Prest, K. W., Jr. 1971. Fundamentals of sexual maturation, spawning, and fecundity of thread herring (*Opisthonema oglinum*) in the eastern Gulf of Mexico. Unpubl. manuscr., Natl. Mar. Fish. Serv., NOAA, St. Petersburg Beach, Fla.

Larval Abundance

Larval abundance varied annually and seasonally (Table 7; Figure 7); the greatest abundances being observed in 1973 and 1974 cruises. Abundance estimates for cruises in which larvae occurred, ranged from 0.20 to 16.63 $\times$ 10^{10} larvae. Estimated annual abundances of larvae were low in 1971 and 1972, but increased in 1973 (Figure 8). No annual estimates were available for 1974, but the great abundance of larvae from cruise CL7412 (Figure 7) suggests that more larvae were present in that year than in any previous year. The increases in larval abundance between 1971 and 1974 are further evidence that spawning intensity increased during the period.

Some scaled sardines as long as 30 mm SL were collected but few larvae longer than 20 mm were taken, and only larvae from 1.1 to 20.0 mm are included in the length–frequency distributions. Most larvae of 1.1 to 3.0 mm were distorted from collection and preservation. Scaled sardine larvae are 2.4 mm at hatching, but within 15 h their length increases to more than 4.0 mm, mostly due to straightening of the body axis rather than true growth (Houde et al. 1974). The most abundant larvae were 2.1 to 4.0 mm in 1972–74, but were larger in 1971 (Figure 7) when towing speed was faster (Houde 1977a) and mesh escapement by small larvae may have been greater.

The ratio of night-caught to day-caught scaled sardine larvae increased slowly as larvae increased in length. No larvae longer than 18.0 mm were sampled during daylight hours. An exponential model $R = 0.7999e^{0.0550X}$ was fitted to the data (Figure 9), where R is the ratio of night-caught to day-caught larvae and X is standard length. It provided the correction factor R, by which daytime catches were adjusted to obtain abundance estimates of larvae by 2-mm length classes in each station area (equation 11, Houde 1977a).

An exponential decrease in abundance of larvae was observed in 1973 (Figure 8) and the larval mortality rate was estimated from these data. Larvae longer than 3.0 mm were assumed to be fully vulnerable to the sampling gear. Abundances (Figure 8) were previously corrected for daytime avoidance.An exponential function was fitted to the data, and the instantaneous rate of decline in abundance per millimeter increase in length was estimated for larvae from 3.1 to 20.0 mm SL. The instantaneous coefficient, Z = 0.3829, is a measure of larval mortality, if gear avoidance was not too great for larval length classes in the analysis. The 0.95 confidence limits on Z are $Z \pm 0.0833$. The observed coefficient corresponds to a 31.8% decrease in larval abundance per millimeter increase in length. Although mortality was not estimated for 1972 larvae, the high estimated abundance of larvae longer than 10 mm (Figure 8) indicates that survival may have been relatively good in that year.

TABLE 7.—Abundance estimates of scaled sardine larvae for each cruise. Estimates include larvae in all size classes and were obtained using equations (2) and (3) (Houde 1977a).

Cruise	Area represented by the cruise ($m^2 \times 10^9$)	Positive area[1] ($m^2 \times 10^9$)	Cruise larvae abundance[2] (larvae $\times 10^{10}$)
GE7101	25.79	0.77	0.00
8C7113 and TI7114	120.48	18.32	8.11
GE7117	101.10	7.93	0.00
8C7120 and TI7121	189.43	13.41	0.39
GE7127, TI7131 and 8B7132	72.99	0.00	0.00
8B7201 and GE7202	148.95	0.00	0.00
GE7208	124.88	27.56	1.85
GE7210	48.43	15.60	2.89
IS7205	104.59	4.88	0.17
IS7209	149.80	0.00	0.00
IS7303	149.80	3.05	0.01
IS7308	151.42	43.38	14.02
IS7311	156.50	25.43	0.92
IS7313	153.18	40.79	16.63
IS7320	153.89	0.00	0.00
CL7405	52.00	5.84	0.20
CL7412	91.33	43.45	13.19

[1]Positive area is defined as the area representing stations where either eggs or larvae of scaled sardines were collected.
[2]Values are not adjusted for cruises that did not encompass the entire area, nor have estimates been corrected to account for gear avoidance by larvae at stations sampled in daylight.

Mortality relative to age of larvae was determined assuming an exponential model of growth for scaled sardine larvae, based on evidence from laboratory rearing experiments. Mean daily growth increments of scaled sardine larvae reared at temperatures above 26°C exceeded 0.5 mm, and frequently were in the range of 0.7 to 1.0 mm (Houde and Palko 1970; Saksena and Houde 1972; Saksena et al. 1972). Methods to estimate age at length and mortality have been reported (Houde 1977a).

Mean egg stage duration for scaled sardine is about 0.81 day. In 1973 the nonfully vulnerable length classes were 1.1 to 3.0 mm. Duration of that larval stage is from 1.0 to 3.0 days based on laboratory experiments (Saksena and Houde 1972; Houde et al. 1974).

An example of duration-corrected abundance data at estimated mean ages for eggs and larvae up to 20.0 mm in 1973 is given in Table 8. In this example the mean daily growth increment was

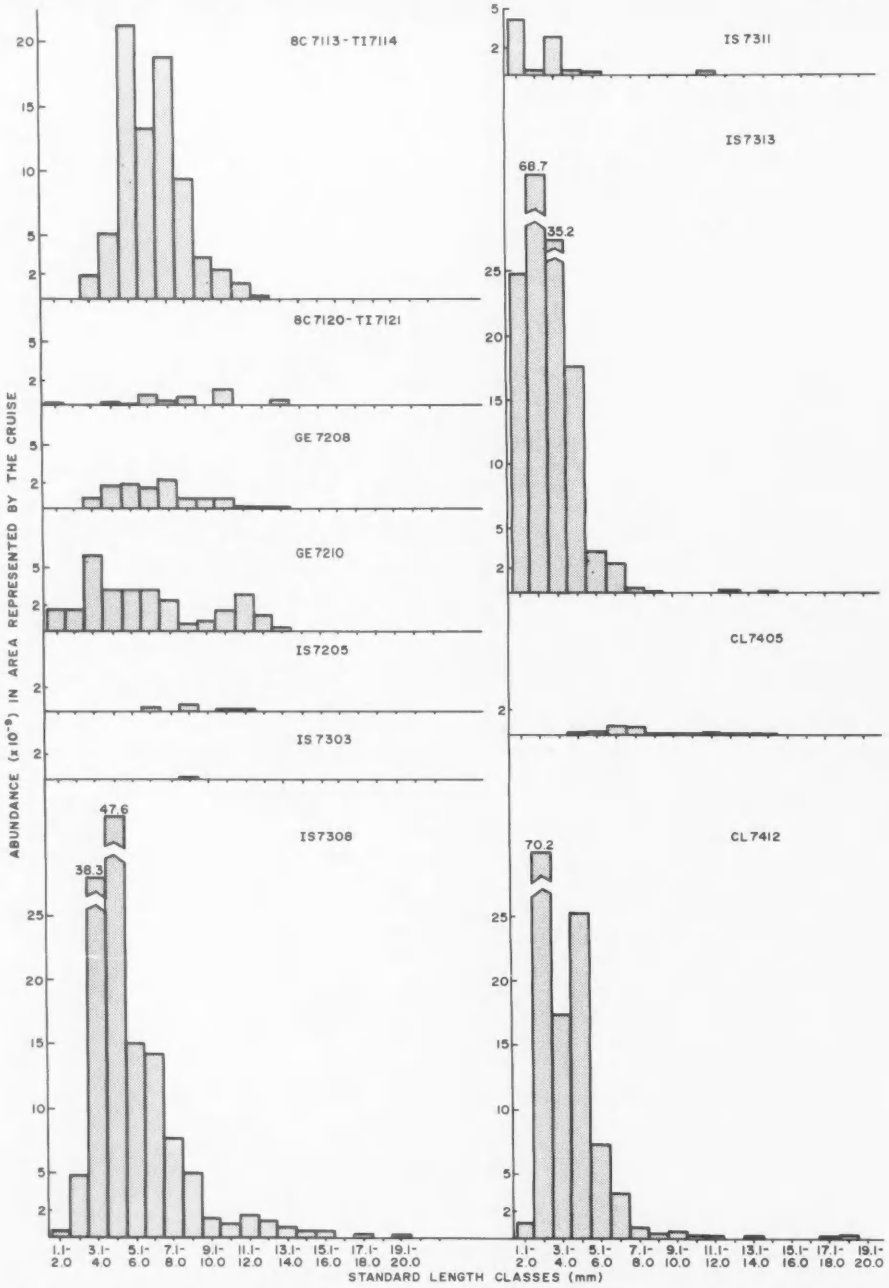

FIGURE 7.—Length–frequency distributions of scaled sardine larvae for 1971–74 cruises to the eastern Gulf of Mexico. Frequencies are expressed as estimated abundance of larvae in each length class within the area represented by the cruise. No adjustments for abundance have been made for cruises that did not cover the entire area where scaled sardine larvae might occur.

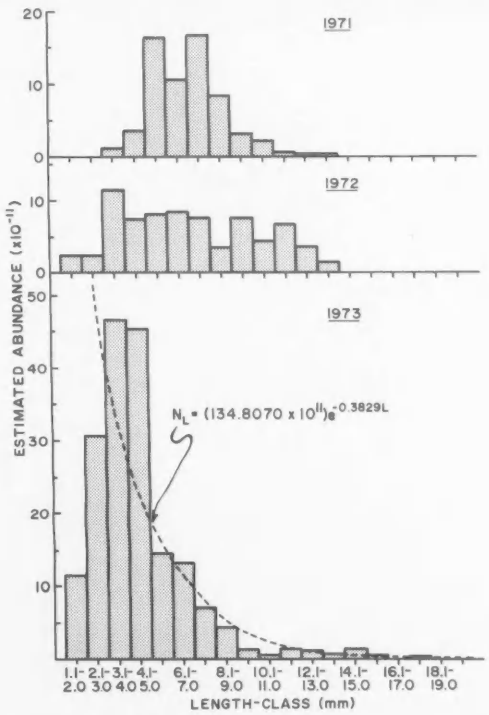

FIGURE 8.—Length–frequency distribution of annual larval abundance estimates for scaled sardine larvae collected in the eastern Gulf of Mexico, 1971–73. Frequencies in each 1-mm length class are expressed as estimated annual abundance and have been corrected for daytime avoidance. A fitted exponential function for 1973 data provides an estimate of the instantaneous coefficient of decline in abundance by length.

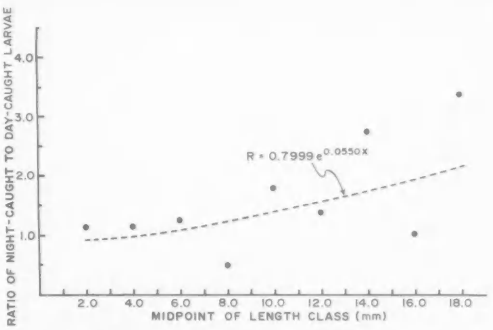

FIGURE 9.—Night to day ratios of sums of catches, standardized to numbers under 10 m² of sea surface, for scaled sardine larvae collected in 1971–74 in the eastern Gulf of Mexico. The ratios were calculated for larvae within each 2-mm length class from 1.1 to 19.0 mm SL. A fitted exponential regression describes the relationship. Larval abundance estimates for each length class at stations occupied during daylight were corrected by the appropriate ratio factor for each length class to account for daytime avoidance.

TABLE 8.—An example of data from 1973 used to obtain stage duration, mean age, and duration-corrected abundance of scaled sardine eggs and larvae. Duration-corrected abundances were subsequently regressed on mean ages to obtain mortality rates (Table 9). Abundance estimates in the second column of the Table were previously corrected for daytime avoidance. In this example, the mean daily growth increment ($\bar{b}$) was set at 0.80. The nonfully vulnerable size classes were 1.1 to 3.0 mm. Calculating procedures were given in Houde (1977a), equations (12) to (16). The regression for these data is presented as Figure 10.

Stage	Abundance (no. × 10^{11})	Duration (days)	Mean age (days)	Duration-corrected abundance (no. × 10^{11})
Eggs	827.54	0.81	0.41	1,025.83
1.1– 3.0 mm	43.27	1.00	1.33	43.27
3.1– 4.0	46.63	2.89	3.21	16.14
4.1– 5.0	45.49	2.25	6.06	20.23
5.1– 6.0	14.71	1.84	8.33	7.99
6.1– 7.0	13.20	1.56	10.22	8.47
7.1– 8.0	7.25	1.35	11.84	5.36
8.1– 9.0	4.52	1.19	13.26	3.79
9.1–10.0	1.45	1.07	14.52	1.35
10.1–11.0	0.84	0.97	15.66	0.87
11.1–12.0	1.65	0.88	16.69	1.87
12.1–13.0	1.24	0.81	17.63	1.52
13.1–14.0	0.83	0.75	18.50	1.11
14.1–15.0	1.56	0.70	19.31	2.23
15.1–16.0	0.61	0.66	20.07	0.93
16.1–17.0	0.05	0.62	20.78	0.09
17.1–18.0	0.39	0.58	21.44	0.68
18.1–19.0	0.00	0.55	22.07	—
19.1–20.0	0.04	0.52	22.67	0.07

set at 0.8 mm and nonfully vulnerable larval stage duration was 1.0 day. I believe that those values are the best estimates for scaled sardine larvae, but other values also were assigned from which both mean ages and duration-corrected abundances were generated. Duration-corrected abundances (Table 8) were regressed on mean ages in an exponential regression to estimate the instantaneous mortality coefficient (Z) for age in days.

Mortality coefficients were calculated for various combinations of mean daily growth increments and durations of the nonfully vulnerable larval stage for 1973 data (Table 9). Possible values of the mortality coefficient, Z, range from 0.1822 to 0.3471, which correspond to daily percentage losses of 16.7 to 29.3%. For data from Table 8, where mean daily growth increment was 0.8 mm and nonfully vulnerable larval stage duration was 1.0 day, the estimated mortality coefficient is $Z = 0.2835$, corresponding to a 24.7% daily loss rate (Figure 10). The most probable scaled sardine mortality estimate for abundance at age data, $Z = 0.2835 \pm 0.0754$ at the 0.95 confidence level, is similar to those for thread

TABLE 9.—Summary of mortality estimates for scaled sardine larvae from the eastern Gulf of Mexico, 1973. Estimates were obtained from the exponential regression of egg and larvae abundances on mean age. Instantaneous growth and mortality coefficients were calculated for various possible combinations of mean daily growth increment and duration of the nonfully vulnerable larval stages. Egg stage duration was assigned the value 0.81 days. Nonfully vulnerable larval lengths were 1.1 to 3.0 mm SL. Explanation of the estimating method is given in equations (12) to (16) of Houde (1977a).

Mean daily growth increment, b (mm)	Instantaneous growth coefficient, g	Nonfully vulnerable larvae duration (days)	Instantaneous mortality coefficient, Z	Y-axis intercept, N_0 (no. $\times 10^{11}$)	Daily mortality rate, $1 - \exp(-Z)$
0.5	0.0552	1.0	0.1842	97.32	0.1683
0.6	0.0662	1.0	0.2179	116.45	0.1958
0.7	0.0772	1.0	0.2509	136.44	0.2220
0.8	0.0883	1.0	0.2835	157.36	0.2469
0.9	0.0993	1.0	0.3156	179.28	0.2706
1.0	0.1103	1.0	0.3471	202.26	0.2933
0.5	0.0552	3.0	0.1822	131.23	0.1665
0.6	0.0662	3.0	0.2146	164.36	0.1932
0.7	0.0772	3.0	0.2461	200.90	0.2182
0.8	0.0883	3.0	0.2767	240.98	0.2417
0.9	0.0993	3.0	0.3065	284.66	0.2640
1.0	0.1103	3.0	0.3353	332.06	0.2849

herring (Z = 0.2124 in 1971 and Z = 0.2564 in 1973), but higher than those for round herring: Z = 0.1317 in 1971–72 and Z = 0.1286 in 1972–73 (Houde 1977a, b).

The y-axis intercepts (N_0) of the regressions in Table 9 also estimate the number of eggs spawned in 1973. Their values are lower than those calculated by the Sette and Ahlstrom (1948) method for 1973 (Table 4), which is considered the best estimate of annual spawning. A higher than expected mortality rate of eggs or nonfully vulnerable larvae may have caused the discrepancy (Figure 10). Larval mortality, considering only fully vulnerable stages, may be lower than that for the entire egg–larval stage. For data from Table 8 and Figure 10, the mortality coefficient for fully vulnerable 3.1- to 20.0-mm larvae is Z = 0.2458, a daily loss rate of 21.8%.

The numbers of probable survivors at hatching, 5.5 mm, and 15.5 mm were estimated in 1973 for three instantaneous growth rates that likely encompass the true rate for scaled sardine larvae (Table 10). Initial egg abundance was the 1973 estimate from Table 4. The estimated number alive at each stage was calculated from the parameters of the exponential functions (Table 9) and from the estimated age in days at each stage (Table 8).

Mortality was high during the egg and larval stages. An apparent mortality of 85 to 91% occurred between spawning and hatching (Table 10). Less than 2% survived to 5.5 mm, when larvae would have been feeding for 2 days at 26° to 28°C (Houde et al. 1974). More than 99.9% mortality had occurred by 15.5 mm, when larvae were beginning to transform to juveniles. At the most probable growth rate, g = 0.0883, only 5 larvae/10,000 spawned eggs were estimated to have survived to 15.5 mm and 20 days of age in 1973.

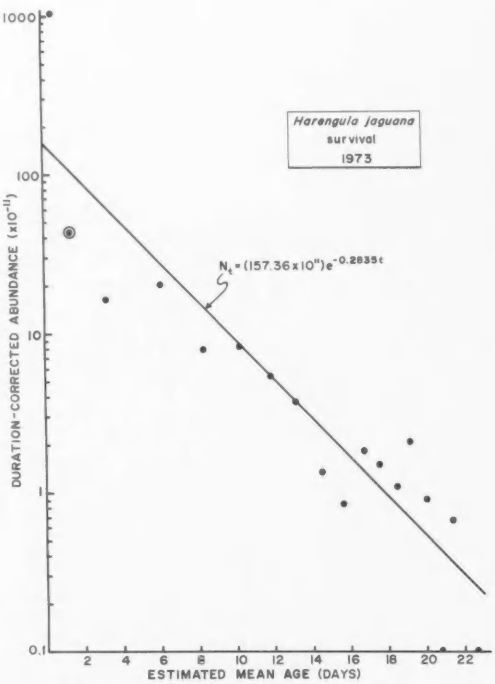

FIGURE 10.—Estimated abundance of egg and larval stages of scaled sardines in the eastern Gulf of Mexico in 1973. Abundance is expressed as a function of estimated age. A fitted exponential function gives an estimate of the instantaneous rate of decline in abundance for eggs and larvae up to 23 days of age. The symbol enclosed in the circle represents the nonfully vulnerable 1.1- to 3.0-mm length classes and was not included in the regression estimate of instantaneous decline.

TABLE 10.—Estimated numbers and percentages of survivors of scaled sardines at hatching, 5.5 mm SL, and 15.5 mm SL in 1973. Estimates are made at three possible growth rates (see Table 9). Duration of the nonfully vulnerable larval stage was set at 1.0 day for 1.1 to 3.0 mm larvae. The number of spawned eggs was based on the estimate in Table 4. Predicted numbers at hatching, 5.5 mm, and 15.5 mm are calculated from exponential functions based on Table 9 data.

Instantaneous growth coefficient, g	Number of spawned eggs ($\times 10^{11}$)	Instantaneous mortality coefficient, Z	Number hatching ($\times 10^{11}$)	Percent mortality[1] to hatching	Number of 5.5-mm larvae ($\times 10^{11}$)	Percent mortality to 5.5 mm	Number of 15.5-mm larvae ($\times 10^{11}$)	Percent mortality to 15.5 mm
0.0662	1,025.83	0.2179	97.61	90.5	11.82	98.8	0.39	99.96
0.0883	1,025.83	0.2835	125.07	87.8	14.83	98.6	0.53	99.95
0.1103	1,025.83	0.3471	152.69	85.1	17.63	98.3	0.68	99.93

[1]Hatching assumed to occur at 0.81 day.

Estimated survival of scaled sardines at hatching and 5.5 mm was lower than that for thread herring or round herring (Houde 1977a, b). In 1973 scaled sardines apparently experienced high mortality during embryonic and young larval stages, which quickly reduced the initial number of eggs to relatively few larvae. Thread herring and scaled sardine mortality rates may be similar for larvae in the fully vulnerable length classes. Round herring larvae had a lower estimated mortality rate than either scaled sardines or thread herring. But, the probable slower growth rate of round herring larvae at cooler temperatures (Houde 1977a) caused estimated numbers at 15.5 mm to be only 40 to 120 survivors/10,000 spawned eggs, which was comparable with the thread herring estimate of 60 to 200 survivors/10,000 eggs, but higher than the 5 survivors/10,000 eggs estimated for scaled sardines.

SUMMARY

1. Scaled sardines spawned from January to September in the eastern Gulf of Mexico, with most spawning occurring during spring and summer. They spawned in waters <30 m deep, mostly within 50 km of the coast.

2. Eggs were collected where surface temperatures ranged from 20.8° to 30.7°C and surface salinities were 29.9 to 36.9‰. Larvae ≤5.0 mm SL were collected at surface temperatures from 18.4° to 30.5°C and at surface salinities of 27.3 to 36.9‰. Most eggs and ≤5.0-mm larvae occurred where surface temperature exceeded 24°C and surface salinity was above 35‰.

3. Estimates of annual spawning increased in each year, 1971–73. Biomass estimates increased from 16,000 to 390,000 metric tons during those years. The mean biomass estimate for the 3-yr period was 184,527 metric tons. Concentrations of adult biomass between the coast and the 30-m depth contour were: 1971—2.8 kg/ha; 1972—24.7 kg/ha; 1973—64.8 kg/ha.

4. Estimated annual potential yields to a fishery were: 1971—4,177 to 8,354 metric tons; 1972—37,064 to 74,128 metric tons; 1973—97,153 to 194,305 metric tons. Potential yield, based on the 3-yr mean biomass estimate, was between 46,132 and 92,264 metric tons, or 7.7 to 15.4 kg/ha.

5. Larvae were more abundant in 1973 than in 1971 or 1972. Larval mortality, relative to length and to estimated ages, was estimated for 1973 data. For length, the instantaneous coefficient was $Z = 0.3829$, corresponding to a 31.8% decrease in larval abundance per millimeter increase in length. For age, the most probable estimate is $Z = 0.2835$, which corresponds to a 24.7% daily loss rate.

6. It is probable that more than 99.9% mortality occurred between spawning and the 15.5-mm stage in 1973. Only 5 larvae/10,000 spawned eggs were estimated to have survived to 15.5 mm at 20 days of age in that year.

ACKNOWLEDGMENTS

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NOTES

REPRODUCTIVE PARAMETERS OF THE OFFSHORE SPOTTED DOLPHIN, A GEOGRAPHICAL FORM OF *STENELLA ATTENUATA*, IN THE EASTERN TROPICAL PACIFIC, 1973–75

Perrin et al. (1976) presented estimates of reproductive parameters of the offshore population of *Stenella attenuata* in the eastern Pacific based on data collected in 1968–73, inclusive. The sample included 3,527 specimens. Only the 1973 sample (2,036) was putatively cross-sectional with respect to age and sex structures of the kill; in earlier years, adult females were selected for examination. The purpose of this paper is to present analyses of samples collected in uniform fashion in 1973, 1974, and 1975, updating the prior report and providing a uniformly developed, albeit short, time series of annual estimates.

Methods and Materials

The data and specimens were collected by NMFS biological technicians aboard commercial tuna vessels. Data collection procedures were the same as described by Perrin et al. (1976). Data on *S. attenuata* were collected on 24 cruises in 1973, 33 in 1974, and 32 in 1975.

The total sample includes 6,243 specimens, 6,168 from precisely known localities (Figure 1). Because of the seasonal nature of the fishery, the sample is heavily biased toward the first half of the calendar year with practically no coverage of the summer months (Table 1).

Laboratory procedures were the same as reported by Perrin et al. (1976), but the analytical methods differed slightly. In calculating gross annual reproductive rate (proportion female × proportion of total females which are reproductive

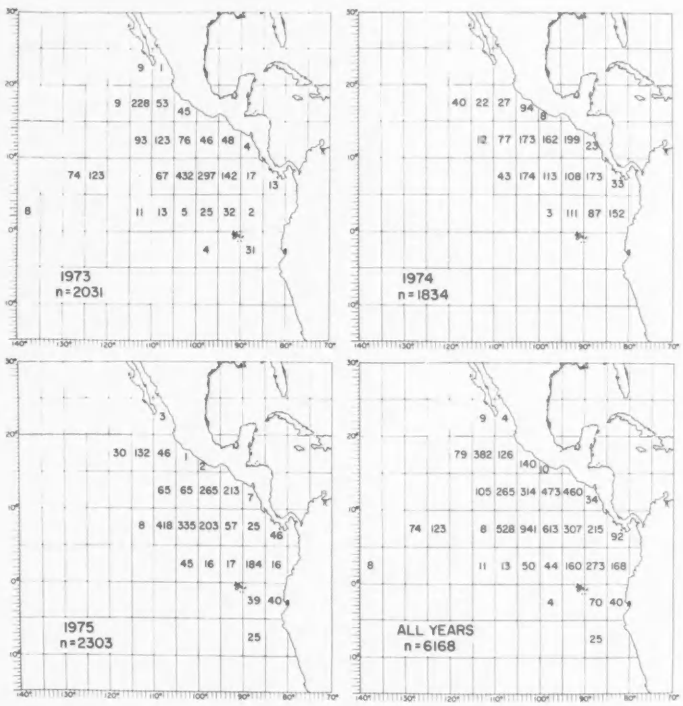

FIGURE 1.—Sample of the offshore spotted dolphin, *Stenella attenuata*, collected in 1973–75, by 5° squares.

TABLE 1.—The sample of the offshore spotted dolphin, *Stenella attenuata*, by sex, year, and month, 1973–75. Date of capture was not available for 18 of the total 6,243 specimens collected.

Month	1973		1974		1975		Total	
	♂	♀	♂	♀	♂	♀	♂	♀
Jan.	267	326	239	300	395	442	901	1,068
Feb.	200	231	428	532	249	312	877	1,075
Mar.	137	210	66	72	133	153	336	435
Apr.	41	46	35	42	135	183	211	271
May	85	156	5	2	34	35	124	193
June	56	69	36	9	30	47	122	125
July	0	0	0	0	6	12	6	12
Aug.	0	0	11	13	2	4	13	17
Sept.	0	0	1	4	0	0	1	4
Oct.	5	16	0	0	31	51	36	67
Nov.	72	103	20	48	32	39	124	190
Dec.	8	9	0	0	0	0	8	9
Totals	871	1,166	841	1,022	1,047	1,278	2,759	3,466
	2,037		1,863		2,325		6,225	

× annual pregnancy rate), Perrin et al. (1976) estimated the proportion of adult females which were reproductive from coloration phase data, based on a subsample of data on percentage mature in the various coloration phases ("mottled" and "fused–adult"). In the present study, a much larger sample of complete reproductive data was available; therefore, the proportion of total females which were reproductive was estimated directly from that sample. Specimens for which ovarian data were lacking or incomplete were allocated to mature or immature categories based on a length criterion. Average length at attainment of sexual maturity was estimated as that length (177 cm) at which the number of shorter but mature specimens in the sample equals the number of longer but immature specimens.

Results and Discussion

Calving Cycle and Pregnancy Rate

The calving cycle, for purposes of analyzing field data, can be divided into three phases: 1) pregnancy, 2) lactation, and 3) "resting" (a catch-all phase for animals neither pregnant nor lactating, which includes females truly resting, i.e., not ovulating because of being between cycles, those which have just ovulated but have not become pregnant, some with extremely small embryos missed in dissection, those which recently aborted, and those which have prematurely terminated lactation due to death of the suckling calf).

We estimated the length of the cycle (and pregnancy rate) in two ways: 1) based on the reproductive structure of the sample of adult females, i.e., based on the assumption that the samples are not biased with respect to reproductive phase, and that the proportion of a sample of mature females in a particular phase is directly proportional to the relative length of that phase, using the previously estimated (Perrin et al. 1976) length of gestation (11.5 mo) as a time calibration, and 2) based on the estimate of length of gestation and a largely independent estimate of length of lactation.

The first estimate was based on data for 1,876 females classified as pregnant, lactating, pregnant and lactating, "resting," or postreproductive (Table 2). The "resting" females were further subdivided into those with and without a corpus luteum. As discussed above, some proportion of those with a corpus luteum can be assumed to represent females not truly resting (with a corpus luteum of infertile ovulation). In the total sample of 3,443 females, 61 were simultaneously pregnant and lactating (6.1% of the lactating females). Minor differences between the numbers in Table 2 and in table 8 of Perrin et al. (1976) reflect increase of the 1973 sample by eight specimens and reexamination and reevaluation of the materials.

Subtraction of the postreproductive females from the aggregate of mature females of determined reproductive condition and allocation of the females both pregnant and lactating to both

TABLE 2.—Reproductive condition of 3,469 female offshore spotted dolphins, *Stenella attenuata*, collected 1973–75.

Condition	1973		1974		1975		1973–75 pooled	
	No.	%	No.	%	No.	%	No.	%
Sexually immature	522	45.0	465	45.9	580	45.7	1,567	45.5
Sexually mature:								
Condition undetermined	58	5.0	60	5.9	191	15.0	309	9.0
Pregnant only	232	20.0	122	12.1	119	9.4	473	13.7
Pregnant and lactating	16	1.4	23	2.3	22	1.7	61	1.8
Lactating only	226	19.5	256	25.3	264	20.8	746	21.7
"Resting"								
With corpus luteum	34	2.9	32	3.2	28	2.2	94	2.7
Without corpus luteum	66	5.7	48	4.7	64	5.0	178	5.2
Postreproductive	7	0.6	6	0.6	2	0.2	15	0.4
Totals	1,161	100.0	1,012	100.0	1,270	100.0	3,443	100.0

categories provides estimates of the proportions of reproductive females in the three phases of the cycle and, comparing the proportions, of the relative lengths of the phases. Estimated average length of the phases and the total cycle can then be calculated for each 1-yr sample and for the pooled samples, based on the relative lengths of the phases and on the estimated gestation period of 11.5 mo (Method 1 in Table 3). The estimates of average length of cycle thus derived trend from 27.3 mo in 1973 to 42.3 mo in 1975, due to increase in the estimated length of lactation from 11.2 mo to 23.3 mo.

Annual pregnancy rate under Method 1 (also in Table 3) is calculated as proportion of reproductive females pregnant divided by the length of gestation (0.958 yr). The reciprocal of annual pregnancy rate is the estimate of average calving interval.

In the second method of calculating length of calving cycle, we estimated length of lactation by assuming that a suckling calf existed in the samples for each lactating female. Under this assumption, the length at which the cumulative frequency of calves in a sample equals the number of lactating females should be the average length at weaning (from which, using the length–age equations published by Perrin et al. (1976), the average age at weaning can be calculated). If the length of lactation increases, the average length at weaning estimated by this method should increase concomitantly. The calculated length at weaning did not increase sharply between years (Table 4). Under Hypothesis II of Perrin et al. (1976) of the rate of deposition of dentinal growth layers (two in first year and one per year thereafter—the most likely alternative), the estimated length of lactation ranges from 11.2 mo in 1973 to 12.4 mo in 1974. To arrive at estimates of the total length of the calving cycle under Method 2, we used the estimate of time spent in the "resting" phase under Method 1 for 1973 (the year for which the two estimates of length of lactation coincide exactly) or 4.6 mo, for each of the three annual estimates. This estimate is based on the assumptions under Method 1 but must suffice as a first approximation. In estimating pregnancy rate (as reciprocal of calving interval)—Table 3—overlapping cycles were taken into consideration by adjusting the effective length of lactation downward by a factor equal to the percentage of lactating females also pregnant.

The 1973 estimate of length of lactation (and length of cycle, pregnancy rate, and calving interval) is very close to that obtained by Method 1 above (11.2 mo), but the two sets of estimates diverge sharply thereafter. The first method could be invalid and cause diverging estimates if 1) lactating females (and their nursing calves) were overrepresented in the samples for 1974 and 1975 or, conversely, 2) either (or both) pregnant or "resting" females were underrepresented. The first situation could obtain if lactating females and their accompanying calves are more likely to be captured and killed in the net because of limited endurance and ability to escape of the calf, certainly less than those of adults, and the strength of the mother–calf bond. The second method could yield erroneous estimates if 1) nursing calves were overrepresented in the samples or,

TABLE 3.—Estimates of lengths of reproductive phases, pregnancy rate, and calving interval under two methods of estimating length of calving cycle (see text) of the offshore spotted dolphin, *Stenella attenuata*, 1973–75.

Item	1973	1974	1975	1973–75 pooled
Sample size (no.)	574	481	497	1,552
Pregnancy (mo)	11.5	11.5	11.5	11.5
Lactation (mo):				
Method 1	11.2	21.9	23.3	17.4
Method 2 (Hyp. II)	11.2	12.4	12.1	11.9
"Resting" (Method 1)	4.6	6.4	7.5	5.9
Sum of phases:				
Method 1				
Months	27.3	39.8	42.3	34.8
Years	2.28	3.32	3.53	2.90
Method 2				
Months	27.3	28.5	28.2	28.0
Years	2.28	2.38	2.35	2.33
Annual pregnancy rate (APR):				
Method 1	0.452	0.314	0.296	0.359
Method 2	0.472	0.459	0.461	0.463
Calving interval (1/APR):				
Method 1				
Years	2.21	3.18	3.38	2.79
Months	26.5	38.2	40.5	33.4
Method 2				
Years	2.12	2.18	2.17	2.16
Months	25.4	26.2	26.0	25.9

TABLE 4.—Estimates of length of lactation in the offshore spotted dolphin, *Stenella attenuata*, based on the cumulative calf length/lactating females method (see text) 1973–75.

Sample	Lactating females[1] (no.)	Length[2] (cm)	Length of lactation			
			Growth layers	Under hypothesis I (mo)	II (mo)	III (mo)
1973	259	135.8	1.86	11.2	11.2	11.2
1974	301	138.5	2.03	12.2	12.4	12.2
1975	376	138.2	2.01	12.1	12.1	12.1
1973–75 pooled	936	137.8	1.98	11.9	11.9	11.9

[1]Includes mature females (≥177 cm) without lactation data prorated to lactating and nonlactating based on proportions in sample with lactation data.
[2]Length at which cumulative number of calves = number of lactating females.

conversely, 2) lactating females were underrepresented. Ongoing analyses of data for the spotted dolphin, *S. attenuata* (J. E. Powers pers. commun.), indicate that small calves are probably overrepresented in small single-set samples. In addition, the absence of sharp change in length of calves at weaning as estimated by the cumulative-calves method speaks against the alternative explanation of development between the years of differential bias against calves and lactating females. The balance of evidence favors the first alternative above, that of progressive overrepresentation of both nursing calves and lactating females as the average number of animals encircled has increased and the average number killed per net haul has decreased[1] accentuating the factor of differential stamina.

Gross Annual Reproduction

Estimates of gross annual reproductive rates can be calculated based on the two methods of estimating pregnancy rate (Table 5). It must be noted that if, as discussed above, small calves are overrepresented in small samples (which make up most of the aggregate sample), then pregnancy rate (and, therefore, gross annual reproductive rate) under Method 1 are underestimated to an unknown, but probably small, degree. This factor, of course, would also cause overestimation of the proportion of the total sample female and the proportion of total females which are reproductive, causing a countering overestimation of gross annual reproduction of unknown, but again probably small, size.

Standard errors are attached to the various estimates where sample size ≥ 100, under the assumption that the binomial distribution tends to normality in large samples (Bailey 1959), allowing calculation of the standard error as:

$$SE = \sqrt{p(1 - p)/n}$$

where p = proportion (estimate of parameter)
n = sample size.

Although gross annual reproductive rate as calculated in Table 5 is a product of three estimates, it can be calculated directly from the total sample (number of females pregnant ÷ total number of males and females), to yield the same estimate and allowing estimation of the variance by the above method. The total sample size was adjusted downward by a factor equal to the proportion of mature females in unknown reproductive condition. The effect on the variance by the constant used to adjust the pregnancy rate to an annual rate was ignored, because the constant (11.5 mo gestation ÷ 12 mo, or 0.958) is close to unity.

The estimates of pregnancy rate (and gross annual reproductive rate) for 1973 and 1974 based on structure of the samples (Method 1) are significantly different from each other (using ±2 SE as an approximation of a 95% confidence interval), and the estimate for 1975, although not statistically different from that for 1974, continues the trend. The estimates based on independent esti-

[1]Staff, Porpoise/Tuna Interaction Program, Oceanic Fisheries Resources Division. 1975. Progress of research on porpoise mortality incidental to tuna purse-seine fishing for fiscal year 1975. SWFC Admin. Rep., Natl. Mar. Fish. Serv., La Jolla, Calif., LJ-75-68, 98 p. (Unpubl. rep.)

TABLE 5.—Calculation of estimates of gross annual reproductive rate of offshore spotted dolphin, *Stenella attenuata*, for 1973–75, using two alternative estimates of pregnancy rate (see text). Standard error follows estimate (see text).

	A	B	C		A × B × C	
			Annual pregnancy rate		Gross annual reproductive rate	
Year	Proportion female	Proportion of females reproductive	Method 1	Method 2	Method 1	Method 2
1971			0.546 (86)			
1972			0.465 ± 0.023 (455)			
1973	0.572 ± 0.011 (2,037)	0.544 ± 0.015 (1,161)	0.452 ± 0.021 (574)	0.472 ± 0.021 (574)	0.141 ± 0.008 (2,036)	0.147 ± 0.008 (1,934)
1974	0.548 ± 0.012 (1,863)	0.535 ± 0.016 (1,012)	0.314 ± 0.021 (481)	0.459 ± 0.023 (481)	0.092 ± 0.007 (1,860)	0.135 ± 0.008 (1,750)
1975	0.559 ± 0.010 (2,321)	0.542 ± 0.014 (1,270)	0.296 ± 0.020 (523)	0.461 ± 0.022 (523)	0.087 ± 0.006 (2,321)	0.140 ± 0.007 (2,001)
1973–75	0.560 ± 0.006 (6,221)	0.541 ± 0.008 (3,443)	0.359 ± 0.012 (1,578)	0.463 ± 0.012 (1,578)	0.109 ± 0.004 (6,243)	0.140 ± 0.004 (5,685)

mates of lengths of gestation and lactation also trend downward, but the year-to-year differences are not statistically significant. As discussed above, the balance of evidence favors the (relatively nonvarying) estimates based on Method 2.

Although adequate data for estimating sex ratio and proportion of total females which were reproductive in 1971 and 1972, using the methods employed here, or for estimating pregnancy rate using Method 2, are not available because of selection of adult females for dissection, the estimates of pregnancy rate (using Method 1) for those two years are included in Table 5. The sample for 1971 is too small to allow direct statistical comparison with the estimates for later years, but the 1972 estimate is not significantly different from the estimates for 1973, reinforcing the suggestion that a major shift in population structure or (more likely) in degree of representativeness of the kill or the sample occurred in 1974.

In summary, the balance of evidence indicates that, in management of the dolphin/tuna situation, changes in the structure of the dolphin kill, per se, should not be taken to necessarily mean that parallel changes in reproductive rates have occurred. The changes more likely represent sampling artifacts caused by changes in the fishing and dolphin rescue operations.

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THE UPTAKE, DISTRIBUTION, AND DEPURATION OF ^{14}C BENZENE AND ^{14}C TOLUENE IN PACIFIC HERRING, *CLUPEA HARENGUS PALLASI*

This note is a sequel to Korn et al. (1976), where uptake, distribution, and depuration of ^{14}C benzene were examined in striped bass, *Morone saxatilis*, and northern anchovy, *Engraulis mordax*. Like benzene, toluene is a prevalent, water-soluble, and toxic monoaromatic component of petroleum and associated products. According to Anderson et al. (1974a), toluene is second only to benzene as the most abundant aromatic oil component in the water-soluble extracts of southern Louisiana and Kuwait crude oils (6.75–3.36 μl/liter benzine; 4.13–3.62 μl/liter toluene, respectively).

Although levels of the volatile aromatics are thought to be low in areas subject to chronic oil exposure, few actual measurements have been made. Further, if fish can accumulate benzene and if energy is required to metabolize, detoxify, and depurate these aromatics, long-term physiological and population effects are possible.

In this study, a comparison of the uptake, distribution, and depuration of ^{14}C benzene and ^{14}C toluene, at a low sublethal concentration [100 parts per billion (ppb)], was undertaken to determine which of these prevalent aromatics may pose the greatest problem. It was hypothesized that, although toluene is less soluble in seawater (Anderson et al. 1974a), it may be more toxic and exhibit greater accumulation levels and persistence. Our previous work with striped bass and northern anchovy indicated other tissues that should be examined, such as kidney, pyloric caeca, gonad, and intestine, and in the present comparison, residues in the additional tissues were measured. Pacific herring, *Clupea harengus pallasi*, were selected as test animals because of their importance as estuarine and nearshore forage fish for many important recreational and commercial species, including striped bass and chinook salmon.

Methods

Pacific herring were obtained from a San Francisco Bay bait dealer and were transported directly to the Tiburon Laboratory dock. The fish were acclimated under test conditions for at least 2

wk in 2,000-liter tanks. Fish were not in spawning condition.

In each of two separate studies, 10 fish were placed into each of six 660-liter fiber glass tanks and further acclimated for 1 wk before exposure. Salinity and temperature were 24‰ and 9°–11°C, respectively, during the acclimation and test periods. In the first study, fish were exposed to 100 nl/liter (ppb) ^{14}C benzene (4.2 dpm/ng specific activity). In the second study, fish were exposed to 100 nl/liter (ppb) ^{14}C toluene (3.2 dpm/ng specific activity). In both studies, one of the six tanks was a control, with no exposure. Exposures were static (single dose with delining concentration) for 48 h, preceded and followed by a continuous water flow of 2 liters/min.

Water samples for radiometric aromatic analyses were taken from all tanks at 0, 6, 24, and 48 h after initial dosage. Gallbladder, intestine, pyloric caeca, gill, brain, liver, muscle, kidney, and immature male and female gonad tissues were sampled for radiometric analyses at 6 h, then daily for 7 days.

Methods of exposure and radiometric analyses are identical to Korn et al. (1976), except that the tissues from fish exposed to toluene were digested at 50°C for 24 h.

Since accumulation levels in the gallbladder were based solely on radiometric analysis of the ^{14}C present and could include metabolites of the monoaromatics as well as unchanged benzene or toluene, an additional study was made to interpret the residue. Two groups of fish, with six fish per tank, were exposed to 100 nl/liter ^{14}C benzene (1 tank), and 100 nl/liter ^{14}C toluene (1 tank) for 48 h. Exposure was the same as in the above experiments. At the end of the 2-day exposure, the gall bladders were removed, weighed, and extracted with 0.2 ml trifluorotrichloroethane-Freon.[1] The extracts were analyzed for benzene and toluene by gas chromatography (Benville and Korn 1974). Efficiency of extraction was not determined and therefore the gas chromatography analyses were more qualitative than quantitative.

Results and Discussion

There were no mortalities in either exposed or control fish. Unlike herring exposed during spawning condition (Struhsaker 1977), no abnormal behavior was noted, thus immature herring appear less sensitive to exposures than mature herring in spawning condition.

The concentration of benzene and toluene in seawater in all tanks declined linearly ($\hat{Y} = a + bX$ where $\hat{Y}$ = concentration in microliters per liter, a = initial concentration in microliters per liter, b = rate of decline in microliter per liter per hour, and X = time in hours), during the 48-h static exposure, as follows:

Item	*Benzene*	*Toluene*
Total no. samples	20	20
a ($\hat{Y}$-intercept)	0.094997	0.09195
b	−0.0006075	−0.0007587
Percentage of initial concentration remaining:		
24 h	85	80
48 h	69	60

The equation for decline in benzene and toluene is probably a function of the volume of seawater. In earlier studies, at smaller volumes, decline was exponential over the 48-h static exposure. At the volume in these experiments it was linear, but probably would have been exponential over a longer time period. The rate of decline appears to decrease with increasing volume.

In all herring tissues, toluene accumulated to higher levels than did benzene (Table 1), despite the faster loss of toluene compared with benzene from the test solution. Certain trends were common to both aromatic components. The tissue exhibiting the highest accumulation was the gallbladder (3.1 nl/g benzene, 34 nl/g toluene, maximum level). The lowest level of maximum accumulation was found in the immature gonad (0.24 nl/g benzene, 0.44 nl/g toluene). Pyloric caeca and intestine contained varying amounts of bile and therefore had a wide range of ^{14}C activity and a resulting wide variance in calculated concentrations.

Benzene was accumulated up to 31 times the initial water concentration (gallbladder) and toluene reached 340 times the initial water concentration (gallbladder).

In most tissues, and for most components, maximum accumulation levels were reached rapidly. Within 24 h, maximum residues were obtained in all tissues except the gallbladder and pyloric caeca. Toluene accumulated to the maximum level (0.25 days) before benzene peaked (1–2 days) in all tissues except the gallbladder and intestine.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

TABLE 1.—Residues of benzene and toluene and/or metabolites (mean nl/g±SE) accumulated during and after a 48-h exposure to 100 nl/liter (ppb) ^{14}C benzene or 100 nl/liter (ppb) ^{14}C toluene in the tissues of *Clupea harengus pallasi*. Number of samples in parentheses.

Tissue and compound	Time (days) from start of exposure[1]							
	Uptake			Depuration				
	0.25 (6 h)	1	2	3	4	5	6	7
Gallbladder:								
Benzene	0.37±0.075 (4)	2.1±0.71 (5)	3.1±0.48 (5)	2.7±1.5 (3)	0.56±0.30 (3)	0.92±0.79 (4)	0.60±0.14 (4)	0.61 (1)
Toluene	4.6±3.4 (5)	30±11 (5)	27±15 (5)	34±17 (5)	19±9.0 (5)	1.7±0.95 (5)	0.24±0.49 (3)	6.0±4.9 (2)
Intestine:								
Benzene	0.83±0.78 (4)	0.42±0.28 (5)	0.61±0.55 (5)	0.16 (1)	—[2] —	0.087 (1)	0.081 (1)	— —
Toluene	3.9±2.4 (5)	2.3±2.1 (4)	2.1±1.7 (5)	0.70±0.7 (5)	0.09±0.014 (2)	0.092±0.013 (3)	0.11±0.025 (2)	0.13±0.70 (3)
Pyloric caeca:								
Benzene	0.058±0.34 (5)	0.63±0.38 (5)	0.64±0.38 (5)	0.095±0.039 (3)	— —	0.056 (1)	— —	— —
Toluene	3.6±3.6 (5)	1.8±0.32 (5)	2.4±1.4 (5)	0.77±0.46 (5)	0.23±0.94 (5)	0.13±0.03 (5)	0.11±0.037 (5)	0.16±0.081 (4)
Gill:								
Benzene	0.51±0.12 (5)	0.61±0.33 (5)	0.73±0.46 (5)	0.073 (2)	0.068 (1)	— —	— —	— —
Toluene	1.8±0.58 (5)	1.2±1.2 (5)	1.0±0.96 (5)	0.20±0.12 (5)	— —	— —	— —	— —
Brain:								
Benzene	0.74±0.11 (5)	0.75±0.14 (5)	0.62±0.052 (5)	0.59 (2)	— —	— —	— —	— —
Toluene	2.1±0.19 (5)	2.0±0.28 (5)	1.5±0.18 (5)	0.13±0.073 (3)	— —	— —	— —	— —
Liver:								
Benzene	0.45±0.070 (5)	0.53±0.096 (5)	0.50±0.067 (4)	— —	— —	— —	— —	— —
Toluene	1.5±0.44 (5)	1.4±0.44 (5)	1.2±0.13 (5)	0.36±0.15 (5)	0.23±0.05 (4)	— —	— —	— —
Muscle:								
Benzene	0.41±0.22 (5)	0.63±0.36 (5)	0.44±0.33 (4)	0.035 (1)	0.066 (1)	— —	— —	— —
Toluene	1.3±0.80 (5)	0.52±0.28 (5)	0.66±0.71 (5)	0.33 (2)	— —	— —	— —	— —
Kidney:								
Benzene	0.32±0.066 (5)	0.32±0.066 (5)	0.40±0.12 (5)	— —	— —	— —	— —	— —
Toluene	1.3±0.50 (5)	1.1±0.40 (5)	0.75±0.33 (5)	0.18±0.099 (4)	— —	— —	— —	— —
Gonad:								
Benzene	0.15±0.021 (5)	0.24±0.062 (5)	0.21±0.10 (5)	— —	— —	— —	— —	— —
Toluene	0.43±0.24 (5)	0.44±0.21 (5)	0.44±0.28 (4)	0.16 (1)	— —	— —	— —	— —

[1]Exposure terminated after 2 days; then fish remained in flowing seawater for 5 days.
[2]— = nondetectable levels.

Residues were depurated rapidly, with most tissues having nondetectable amounts after 3–4 days (1–2 days after termination of exposure). The gallbladder, intestine, and pyloric caeca retained residues through the duration of the study (7 days).

In the experiment in which gas chromatographic analyses were performed on the gallbladder, no detectable benzene (<0.1 nl/g) was measured. Gas chromatography analysis resulted in only 0.56–1.5 nl/g toluene. This indicates that most or all of the radioactivity measured by liquid scintillation in the gallbladders of fish exposed to benzene is not the parent compound, but one or more metabolites. Fish exposed to toluene had a small amount of the parent compound as opposed to metabolites (1.5 nl/g toluene maximum, compared with 27 nl/g expected [Table 1]).

The above result and the occurrence of delayed depuration in the gallbladder, intestine, and pyloric caeca supports the contention that benzene and toluene are metabolized in the liver, stored in the gallbladder, then passed into the intestine and are excreted with the feces. This agrees with Roubal et al. (in press) who found high levels of benzene metabolites in the liver and gallbladder of salmon which had previously received intraperitoneal benzene injections. This also agrees with our previous results with benzene in other fishes (Korn et al. 1976), results of Neff (1975), and with work by Lee et al. (1972) who demonstrated metabolism of polycyclic aromatics in the liver

and subsequent storage in the gallbladder. Studies with polycyclic aromatics (naphthalene, benzpyrene) by other investigators (Lee et al. 1972; Anderson et al. 1974b; Neff 1975; Roubal et al. in press) indicate higher accumulation levels and slower depuration than we have found with benzene and toluene. However, different species are involved, and these higher aromatics are also less prevalent in the water-soluble extract of crude oil.

The results of this study are generally consistent with our previous work exposing striped bass and northern anchovy to ^{14}C benzene at the same initial concentration and exposure period (100 nl/liter for 48 h; Korn et al. 1976), except for the considerably higher accumulation in the anchovy than in the other species. This is probably primarily a result of the higher stress, activity level, and scale and mucus loss in anchovy while in captivity.

The gonads sampled in this study were immature and showed low accumulation levels. In another study exposing mature spawning herring to 100 nl/liter benzene for 48 h (Struhsaker 1977), higher accumulation occurred in the ovary, with associated deleterious effects on the ripe ovarian eggs and on development of larvae subsequent to exposure of the parental females.

Of the two components studied here, toluene would appear to be potentially a greater problem to fish. Toluene could be rapidly accumulated to high levels in fish after even a brief contact during an oil spill. Since toluene is one of the more prevalent water-soluble oil components, further research on the effects and uptake of this component are indicated. Further, chronic exposures are probably of more importance to the survival of fish populations than are spills, and studies of long-term exposure to chronic concentrations should be made.

Finally, the probability that benzene and toluene are rapidly metabolized or converted to metabolites (possibly phenol, which is also highly toxic) leads to the need for metabolite research. Uptake studies with phenolic metabolites would be of interest, as would be the determination of uptake over extended time intervals.

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FOOD HABITS AND FEEDING CHRONOLOGY OF RAINBOW SMELT, *OSMERUS MORDAX*, IN LAKE MICHIGAN[1]

Rainbow smelt, *Osmerus mordax* Mitchill, in Lake Michigan originated from a planting in Crystal Lake, Mich., in 1912 (Van Oosten 1937). Since its introduction in Lake Michigan, the smelt has become abundant, serving as forage for larger, predatory species (Wright 1968; Harney and Norden 1972) and sustaining a small seasonal sport and commercial fishery. There has been considerable controversy regarding the smelt's role as a piscivore. Food studies of smelt in Saginaw Bay, Lake Huron (Gordon 1961) and Lake Erie (Price 1963) have shown that smelt consumes fishes, but not the alewife, *Alosa pseudoharengus*. Recently, a fall collection of smelt revealed that it consumes young-of-the-year alewives (O'Gorman 1974).

The food habits of Lake Michigan smelt have not been studied on a seasonal basis and little information exists concerning its food habits during the winter months. Also, feeding chronology has never been considered. The purpose of this study was to examine food habits of smelt during 6 mo representing all four seasons and to consider feeding chronology during two representative months.

Materials and Methods

Rainbow smelt were collected along the western shore of Lake Michigan by gillnetting or trawling on six dates between March 1973 and June 1974 (Table 1). Gill nets were placed on the bottom overnight and 45-min trawl hauls performed at 4-h intervals over a 24-h period. Gill nets were set and retrieved at 4- to 6-h intervals over a 24-h period on 13 October 1973 in order to examine feeding chronology. Smelt were collected at different depths during the course of the study because of their seasonal inshore–offshore movements. Fish were frozen shortly after capture.

Feeding chronology was examined on 23 March and 13 October 1973. Stomachs of smelt used in this portion of the study were dissected out and the contents removed. Fish and stomach contents were dried for 48 h at 60°C and weighed to the nearest milligram. Dried stomach contents were expressed as a percentage of dry body weight. The significance of time of day on the amount of food in stomachs was ascertained with analysis of variance (ANOVA). Means and the ANOVA were calculated from arcsine transformed data (Sokal and Rohlf 1969). A chi-square contingency test was used to ascertain the significance of time of day on the occurrence of empty stomachs. Significance testing was performed at the 0.05 error level.

TABLE 1.—Dates, locations, depths, and methods of capture of Lake Michigan smelt examined in this study.

Collection date	Location (off shore from)	Depth (m)	Method of capture[1]
20 Feb. 1974	Algoma, Wis.	85	Gill net
23 Mar. 1973	Two Rivers, Wis.	74	Bottom trawl[2]
21 May 1974	Milwaukee, Wis.	18	Gill net
18 June 1974	Milwaukee, Wis.	18	Gill net
15 Aug. 1974	Milwaukee, Wis.	27	Gill net
13 Oct. 1973	Port Washington, Wis.	37	Gill net[2]

[1]All collections made on the bottom.
[2]Feeding chronology examined.

Separate smelt were examined for food habits. These fish were measured to the nearest millimeter in length. Stomachs were removed, contents of each stomach were placed in a Petri dish with water, and the organisms enumerated. Food habits were defined in terms of percentage numbers and percent dry weight of stomach contents (Wells and Beeton 1963). Dry weight indices used were fish, 176; *Mysis*, 3; *Pontoporeia*, 1; fingernail clam, 1; Tendipedidae, 0.4; and Cladocera-Copepoda, 0.003 (Morsell and Norden 1968).

Results

Stomachs of 515 smelt were examined. Food of smelt included *Mysis; Pontoporeia;* alewives (young-of-the-year and yearlings); and to a lesser extent, fingernail clams; Tendipedidae pupae; cladocerans; and copepods (Table 2, 3). A marked increase in piscivorous food habits was observed in smelt longer than 180 mm. For this reason, smelt were divided into two size groups.

Smelt shorter than 180 mm consumed primarily *Mysis* during October, February, and March (Table 2). Smelt were found in shallower water during May, June, and August and their stomachs contained yearling alewives, *Pontoporeia,* and Tendipedidae. *Pontoporeia* were consumed most frequently during August, when they represented 35% dry weight of the diet. Tendipeds represented 25, 6, and 2 percentage numbers of the diet during May, June, and August, respectively. However,

[1]This research was supported by the University of Wisconsin Sea Grant Program. Contribution No. 154, Center for Great Lakes Studies, University of Wisconsin-Milwaukee, Milwaukee, Wis.

TABLE 2.—Food habits of Lake Michigan smelt shorter than 180 mm total length. Upper values for food organisms represent dry weight and values in parentheses are the percentage numbers.

Collection date	Average and range of lengths (mm)	No. of stomachs examined	% of stomachs empty	Food organisms					
				Mysis	*Ponto-poreia*	Alewife	Fingernail clam	Tendi-pedidae	Copepoda and Cladocera
20 Feb. 1974	147	79	42	98	1	—	1	—	—
	90–179			(95)	(3)		(2)		
23 Mar. 1973	138	80	36	100	—	—	—	—	—
	94–179			(100)					
21 May 1974	162	68	60	62	<1	37	<1	1	—
	109–179			(73)	(1)	(1)	(1)	(25)	
18 June 1974	160	62	61	42	—	58	—	<1	<1
	140–179			(12)		(1)		(6)	(82)
15 Aug. 1973	157	40	1	30	35	30	5	<1	<1
	120–175			(26)	(61)	(1)	(9)	(2)	(2)
13 Oct. 1973	158	88	34	87	3	10	<1	—	—
	115–179			(88)	(9)	(1)	(2)		
Total	154	417	41	70	7	23	1	<1	<1
				(66)	(12)	(<1)	(2)	(6)	(14)

TABLE 3.—Food habits of Lake Michigan smelt 180 mm total length and longer. Upper values for food organisms represent percent dry weight and values in parentheses are the percentage numbers.

Collection date	Average and range of lengths (mm)	No. of stomachs examined	% of stomachs empty	Food organisms			
				Mysis	*Ponto-poreia*	Alewife	Finger-nail clam
20 Feb. 1974	210	21	43	39	1	60	—
	180–251			(93)	(5)	(2)	
23 Mar. 1973	206	20	25	95	5	—	—
	180–246			(86)	(14)		
21 May 1974	199	27	37	6	—	94	—
	181–238			(78)		(22)	
18 June 1974	206	10	60	1	—	99	—
	196–232			(33)		(66)	
15 Aug. 1973	201	8	12	93	6	—	1
	182–225			(82)	(16)		(1)
13 Oct. 1973	201	12	42	12	1	87	1
	181–248			(75)	(14)	(9)	(2)
Total	204	98	37	41	2	57	<1
				(75)	(8)	(17)	(<1)

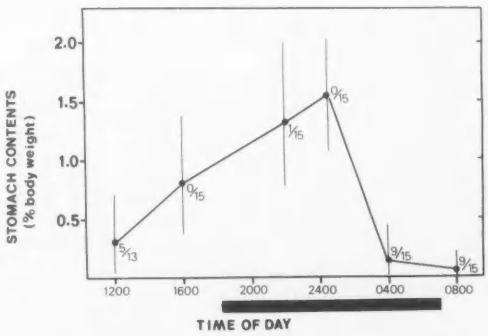

FIGURE 1.—Feeding periodicity of Lake Michigan smelt collected on 13–14 October 1973. Dry weights of stomach contents are expressed as a percentage of dry body weight. Vertical lines represent ±2 SE of the mean and the horizontal black bar the hours of darkness. The number of empty stomachs and number of stomachs examined are given near each average.

these numbers never exceeded 1% dry weight of the diet. Alewives were consumed most frequently during the June collection when yearlings composed 58% dry weight of the diet. Small alewives constituted 30 and 10% dry weight of the diet during August and October, respectively.

Food eaten by smelt 180 mm and longer consisted principally of small alewives and *Mysis*, but included small numbers of *Pontoporeia* and occasionally fingernail clams (Table 3). Yearling alewives represented 94 and 99% dry weight of the diet during the May and June collections, respectively.

Smelt examined for feeding periodicity averaged 158 mm total length. Weight of stomach contents differed statistically over the 24-h period during the October collection ($F = 9.99$, $P \leq 0.001$, df = 5, 82). Stomachs contained the most food (1.5% body weight) at 2430 h and decreased to 0.2% by 0400 h (Figure 1). In addition, the occurrence of empty stomachs was dependent upon time of day ($\chi^2 = 31.51$, $P \leq 0.001$, df = 5). Only 1 out of 45 stomachs was empty in the collections between 1600 and 2430 h. In contrast, 23 out of 43 stomachs were empty between 0400 and 1200 h (Figure 1). The March collection showed no significant differences in weight of stomach contents over a 24-h period.

Discussion

Smelt examined in this study were piscivorous, consuming young-of-the-year and yearling alewives. Food habit studies of smelt in Saginaw Bay, Lake Huron (Gordon 1961) and Lake Erie (Price 1963) have shown that smelt consume fishes, but not alewives. Smith (1970) hypothesized that dif-

ferences in their depth distributions could explain failure to demonstrate predation of smelt upon alewives. Recently, smelt collected from northern Lake Michigan during the fall were reported to contain large numbers of young-of-the-year alewives in their stomachs (O'Gorman 1974). Smelt examined in this study consumed alewives not only during the fall, but also during February, May, June, and August. This study and O'Gorman's confirm the smelt's role as a predator of alewives in Lake Michigan. The high frequency of small alewives and *Mysis* in the diet of smelt suggests a preference for larger food items.

Increased piscivority with size is well known among predatory fishes. Lake Erie smelt longer than 126 mm consumed more fishes than smaller specimens (Price 1963). In this study, smelt 180 mm and longer consumed about three times more fish than the smaller individuals (grand averages of 57 and 23%, respectively). According to O'Gorman (1974), the smallest smelt which had consumed a fish was 143 mm total length. In the present study, the smallest smelt which had consumed an alewife was 157 mm.

Seasonal differences in food habits reflect changes in depth distribution of smelt and annual changes in abundance of prey. Smelt in Gull Lake, Mich., consumed primarily copepods and cladoceran during early winter but from May to August, dipterans were their principal food (Burbidge 1969). Similarly, smelt examined in this study consumed Tendipedidae only during May, June, and August, when the flies were abundant. In Lake Superior, smelt longer than 125 mm consumed mostly *Mysis* except during May and June, when copepods ranked first (Anderson and Smith 1971). Likewise, smelt examined in our study showed a change in food habits from winter to spring but, in this case, from *Mysis* to yearling alewives. Following littoral spawning during April, smelt were captured in shallower water where *Mysis* is not abundant. Schools of small alewives occupying this zone provided an alternative food.

Smelt examined during October fed after dusk and ceased feeding during the night. *Mysis* represented 87% dry weight of the diet during the October collection. This in conjunction with the known fact that *Mysis* undergoes a nocturnal vertical migration (Beeton 1960) suggests that their feeding was associated with the migration, and consequent availability of the smelt's principal food organism. Feeding of young-of-the-year sockeye salmon, *Oncorhynchus nerka*, has been related to diel vertical movements of zooplankton (Narver 1970). A statistically significant feeding periodicity was not demonstrated during the March collection. However, this could be due to reduced feeding intensity as evidenced by very small amounts of food present in their stomachs (e.g., 0.1% body weight).

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USEABLE MEAT YIELDS IN THE VIRGINIA SURF CLAM FISHERY[1]

The weight of surf clam meat landed in Virginia is estimated by the National Marine Fisheries Service, Division of Statistics and Market News (DSMN) by multiplying bushels landed by a constant of 17 lb (7.71 kg) of total meat per bushel. However, total meat weight includes the viscera, a portion of clam not utilized by the industry. Herein is an analysis of the yield of useable surf clam meat weight per bushel and seasonal variability in meat weight relative to seawater temperature for Virginia stocks.

Methods

Monthly mean useable meat weight per bushel (MMUWB) was estimated from 181 daily landings totaling 167,564 bushels in 1974, and 160 daily landings totaling 270,170 bushels in 1975. The surf clams were harvested from Virginia stocks in the region offshore of Cape Henry and south to about False Cape.

Meat weight landings reported by DSMN are in pounds, for conformity useable meat weight estimates are also cited in pounds.

Monthly mean seawater temperature (MMST) was estimated from daily surface water temperatures recorded at Kiptopeke Beach, Va. (lat. 37°10.0′N, long. 75°59.3′W), about 13 n.mi. north of Cape Henry. These data, collected and published by National Oceanic and Atmospheric Administration (NOAA), Oceanographic Surveys Branch, exhibited seasonal trends which were correlated to changes in useable meat yield per bushel. Although these temperatures are not in situ measurements, they are a convenient covariate of meat yield.

The relationship of MMUWB to MMST was estimated by Model II regression analysis since both variables were subject to sampling error. The choice of a particular Model II analysis relative to the source of the variability (measurement errors, inherent variability, or both) is a somewhat unsettled subject recently discussed by Moran (1971), Ricker (1973, 1975) and Jolicoeur (1975). No such theoretical considerations were used in the present analyses. Four models were employed to derive "predictive" equations from the 1974 data: Ricker's (1973) geometric mean analysis (GM regression); Wald's (1940) and Bartlett's (1949) arithmetic mean analysis (termed AM regression by Ricker); and principal axis analysis (although it is recognized that variables do not truly have a bivariate normal association). Empirically, the adequacy of the models in predicting the observed 1975 annual mean useable meat weight per bushel (AMUWB) from the MMST in 1975 was assessed by a randomized block (two-way) analysis of variance in which the predicted and observed MMUWB were the experimental units replicated by months. MMST was recorded to 0.1°C, MMUWB to 0.01 lb.

Results and Discussion

The MMUWB of surf clams ranged from 10.8 to 14.0 lb in 1974, and from 10.6 to 14.5 lb in 1975 (Table 1). AMUWB, 12.5 lb in 1974 and 12.6 lb in 1975, were nearly identical ($P>0.80$). There was a cyclical increase in the MMUWB from the minima in winter months to maxima in July and August 1974 and in July 1975. The correlation coefficients (r) for MMUWB and MMST were 0.64 and 0.79 in 1974 and 1975, respectively; $r = 0.71$ for the pooled data.

The sinusoidal trend in MMUWB is probably related to maturation and subsequent spawning. Ropes (1968) reported a major spawning period in summer and a minor period in fall in New Jersey waters, but the time and duration of surf clam spawning in Virginia waters has not been reported. If increasing MMUWB is indicative of maturation, the data imply that most spawning by

[1]Contribution No. 801, Virginia Institute of Marine Science, Gloucester Point, Va.

TABLE 1.—Number of bushels of surf clams processed, mean weight (pounds) of useable meats per bushel, and mean surface seawater temperature at Kiptopeke Beach by months in 1974 and 1975.

Month	Number of bushels		Mean useable meat/bushel		Mean seawater temperature (°C)	
	1974	1975	1974	1975	1974	1975
Jan.	19,736	18,225	11.7	10.6	6.7	5.9
Feb.	11,791	18,489	12.3	11.3	5.6	5.7
Mar.	13,450	8,237	12.3	12.7	8.4	6.7
Apr.	14,415	23,725	13.3	13.2	12.2	9.8
May	19,020	39,130	13.8	12.9	17.6	17.1
June	12,981	30,049	13.9	13.7	21.7	22.5
July	8,328	19,488	14.0	14.5	24.8	24.6
Aug.	10,140	23,930	14.0	13.7	25.0	26.6
Sept.	14,430	23,038	12.0	13.2	22.9	23.2
Oct.	14,558	29,136	11.4	12.4	16.2	19.5
Nov.	13,388	8,407	10.8	11.8	12.2	14.0
Dec.	15,327	28,316	10.8	11.1	6.8	7.6
Total	167,564	270,170				
Annual mean yield/bushel			12.52	12.59		

Virginia surf clams is from about May or June through August. Loesch[2] reported a size range of 2 to 18 mm for young-of-the-year surf clams in early October 1974 and estimated their age ranged from 1 to 4.5 mo. Thus, spawning in 1974 occurred from at least June through early September.

The regression of MMUWB on MMST for the 1974 data by the four models resulted in the following equations:

$$\text{Wald's AM regression: } \bar{W} = 10.1 + 0.102\,\bar{C}$$
$$\text{Bartlett's AM regression: } \bar{W} = 11.0 + 0.101\,\bar{C}$$
$$\text{Ricker's GM regression: } \bar{W} = 10.0 + 0.168\,\bar{C}$$
$$\text{Principal axis: } \bar{W} = 10.9 + 0.108\,\bar{C}$$

where $\bar{W}$ = MMUWB; $\bar{C}$ = MMST (degrees Celsius); and the first and second values are the intercept and regression coefficients, respectively.

Predicted MMUWB values in 1975 and their respective AMUWB are presented in Table 2. Analysis of variance (Table 3) indicated a significant difference among the predicted and observed AMUWB values ($P<0.001$). The Student-Newman-Keuls multiple range test indicated that the only significantly different AMUWB was that associated with the predicted MMUWB estimates derived from Wald's AM regression. Thus, the other three regression models predicted the AMUWB with equally acceptable precision.

The total useable meat yield obtained from the 270,170 bushels of surf clams processed in 1975 was 3,425,654 lb (1,554 metric tons). The sum of the products of MMUWB and monthly landings for all three acceptable models estimated the total useable meat yield with an error ≤0.5%. For all practical purposes the estimate could have been made by using the 1974 AMUWB of 12.5 lb. Total useable meat estimated with this constant was in error by only 1.4%. However, because of seasonal changes in body weight, monthly total useable meat yields should be derived from the MMUWB predicted by one of the acceptable regression equations.

[2]Loesch, J. G. 1975. Inventory of surf clams in nearshore waters from Cape Henlopen to the False Cape area. Final Rep. 03-4-043-357, U.S. Dept. Commerc., Natl. Mar. Fish. Serv., State-Fed. Fish. Manage. Prog.

TABLE 2.—Mean monthly useable meat weight (pounds) per bushel for Virginia surf clams in 1975 estimates by four regression models.

Month	AM (Wald)	AM (Bartlett)	GM (Ricker)	Principal axis
Jan.	10.7	11.6	11	11.5
Feb.	10.7	11.6	11	11.5
Mar.	10.8	11.7	11.1	11.6
Apr.	11.1	12.0	11.6	12.0
May	11.8	12.7	12.9	12.8
June	12.4	13.3	13.8	13.3
July	12.6	13.5	14.1	13.6
Aug.	12.8	13.7	14.5	13.8
Sept.	12.5	13.4	13.9	13.4
Oct.	12.1	13.0	13.3	13.0
Nov.	11.5	12.4	12.4	12.4
Dec.	10.9	11.8	11.3	11.7
Annual mean yield/bushel	11.65	12.55	12.57	12.55

TABLE 3.—Randomized block analysis of variance of the 1975 observed and predicted mean monthly useable meat weight (pounds) per bushel replicated by months.

Source of variation	Degree freedom	Sum of squares	Mean square	Critical ratio (F)
Months	11	50.96	4.63	
Among models	4	7.97	1.99	
Within models	44	6.84	0.155	12.83*
Total	59	65.77		

*$P<0.001$

The observed AMUWB for the pooled data of 1974 and 1975 is 12.55 lb and can be used if only annual estimates of useable surf clam meat yields for Virginia stocks are desired. If a substantial change in seasonal harvesting occurred, e.g., a closed season, one of the acceptable regression equations should be used until a new AMUWB constant is estimated.

Barker and Merrill (1967) reported losses of 11 to 20% in body weight with the removal of the viscera from New Jersey surf clams. However, they sampled in May and November when the gonadal portion of the viscera is not near its maximum weight. The present data indicate that the reported DSMN yearly landing weights, based on 17 lb of meats per bushel, must be reduced by 26% to more accurately ascertain the weight of Virginia surf clam meats actually shipped to market.

Acknowledgments

I am indebted to Ned Doughty, owner and operator of the C&D Seafood Company, Oyster, Va., who made available his daily surf clam landing and meat yield data for 1974 and 1975. Also, I acknowledge the aid of Charles R. Muirhead, Chief, Oceanographic Surveys Branch, NOAA, who supplied the monthly mean seawater temperature data for Kiptopeke Beach, Va., prior to its publication.

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MERCURY IN FISH AND SHELLFISH OF THE NORTHEAST PACIFIC. III. SPINY DOGFISH, *SQUALUS ACANTHIAS*

The spiny dogfish, *Squalus acanthias* Linnaeus, is a small shark that is abundant in the northeast Pacific and has been utilized both as a food fish and as a source of industrial fishery products. This species was heavily harvested in the 1940's for the high vitamin A content in the liver oil until the population was significantly reduced (Alverson and Stansby 1963). The declining resource, along with the availability and low cost of synthetic vitamin A, led to the collapse of the fishery in the early 1950's. Since that time the dogfish population has significantly increased, but the low economic value of the species precluded development of any substantial fishery.

Another limiting factor in commercial handling of dogfish is its rather rapid deterioration. Stansby et al. (1968) found that rancidity, not bacterial spoilage, was the principal factor limiting the ice-storage life of dogfish. If dogfish are properly iced and handled quickly, off flavors due to rancidity and the breakdown products of urea are minimized, and they can be used as food.

Recently there has been a renewed interest in commercial exploitation of this species in Puget Sound, primarily because of the export demand and increased price for frozen dogfish fillets and bellyflaps in Europe. In 1975 only 0.43 million lb of dogfish were landed in the State of Washington for both food and reduction purposes, in contrast to 4.9 million lb landed during 1976 in Puget Sound ports[1] and processed for export to Great Britain and West Germany. As a result of the current interest in the use of Puget Sound dogfish as food and the mercury levels in relation to import regulations of various countries, this investigation was undertaken to determine the mercury levels in dogfish from inland waters of the State of Washington. This report summarizes our findings.

Materials and Methods

The specimens were obtained from commercial gill net and longline catches through the cooperation of the industry and the State of Washington Department of Fisheries. They were collected from the Strait of Georgia near Blaine, Wash. (Figure 1), and from five locations in Puget Sound: Port Townsend, Port Susan, Seabeck (Hood Canal), Seattle (Elliott Bay), and Tacoma (Tacoma Narrows to Carr Inlet). Date and location of capture, round weight, length, and sex were recorded for each fish. Commercial buyers had established a minimum acceptable length of 32 in (81.3 cm) for food processing; therefore, the size distribution of most samples reflected this market practice rather than the normal range of lengths in the dogfish population.

[1]Preliminary landings data, State of Washington Department of Fisheries.

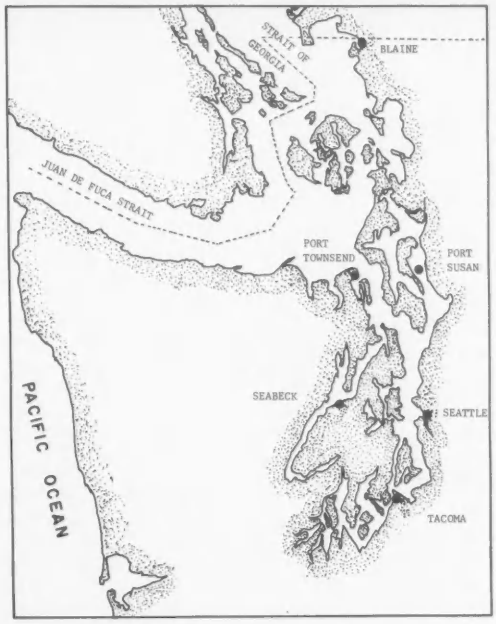

FIGURE 1.—General points of collection of spiny dogfish in Puget Sound and the Strait of Georgia.

Analytical samples were prepared at this laboratory and consisted of the skinned and deboned edible muscle tissue from both fillets and bellyflaps. Since the bellyflaps are marketed as a separate product, they were removed and analyzed separately. Each sample was ground and thoroughly mixed prior to subsampling for analysis.

Total mercury was determined by the U.S. Food and Drug Administration's Vanadium Pentoxide Method (Munns 1972), which uses a nitric-sulfuric acid digestion with vanadium pentoxide as a catalyst. Final determination was by flameless atomic absorption spectroscopy with results stated in parts per million (ppm) of mercury on a wet-weight basis. All samples were subjected to single analysis, and those exceeding 0.40 ppm were repeated. Differences between replicates did not exceed 0.05 ppm. A standard fish sample was analyzed routinely as an internal control.

Results and Discussion

A total of 141 dogfish (127 females, 14 males) were analyzed for mercury content. Mean mercury levels in specimens from each area (Table 1) were at or above the action level of 0.50 ppm set by the U.S. Food and Drug Administration (FDA) (Schmidt 1974). Specimens taken from the west side of Puget Sound (Port Townsend and Seabeck) contained lower levels of mercury than did those taken from the east side of Puget Sound (including Blaine). The mercury levels appeared to increase from north to south on each side of the Sound. This phenomenon may be due to the absence of industry at points of collection on the west side of the Sound and an increase of industrial activity from north to south along the east side of the Sound; however, these observations on the effect of catch area may not be representative of the total Puget Sound dogfish population.

The mean mercury level for the 127 female dogfish fillets was 0.92 ppm, which is almost twice the FDA action level. The mercury level in 91 females (72%) exceeded 0.50 ppm and 48 (38%) exceeded 1.0 ppm. Regression analysis showed a positive correlation between mercury content of

TABLE 1.—Mercury concentration in spiny dogfish from the State of Washington.

						Mercury (ppm)									
						Fillets					Bellyflaps				
		Weight (g)		Length (cm)					>0.5 ppm					>0.5 ppm	
Location	No. of fish	Range	Mean	Range	Mean	No. of fish	Range	Mean	No.	%	No. of fish	Range	Mean	No.	%
						Females									
Port Townsend	22	2,190–4,160	3,194	85–102	93.9	22	0.16–1.28	0.50	9	40.9	20	0.14–1.18	0.41	5	25.0
Seabeck	12	2,465–4,915	3,372	86–106	93.5	12	0.34–1.43	0.63	7	58.3	12	0.29–1.30	0.57	7	58.3
Blaine	20	2,360–5,065	3,469	86–106	94.6	20	0.20–1.38	0.71	15	75.0	20	0.17–1.27	0.62	15	75.0
Port Susan	32	1,340–4,560	3,033	70–106	89.6	32	0.09–2.28	0.89	20	62.5	22	0.17–1.95	1.02	19	86.3
Seattle	8	5,230–7,930	6,706	105–117	109.9	8	0.82–1.94	1.16	8	100.0	—	—	—	—	—
Tacoma	33	700–6,630	3,862	60–113	95.2	33	0.43–2.58	1.41	32	96.9	33	0.38–2.24	1.25	32	96.9
Σ	127	700–7,930	3,608	60–117	94.2	127	0.09–2.58	0.92	91	71.6	107	0.14–2.24	0.85	78	72.9
						Males									
Port Susan	7	1,445–2,645	1,864	75–87	79.4	7	0.21–0.98	0.64	6	85.7	2	0.49–0.95	0.72	1	50.0
Seattle	4	2,025–3,400	2,626	85–93	89.0	4	1.16–1.61	1.38	4	100.0	—	—	—	—	—
Tacoma	3	1,240–2,180	1,728	68–84	77.3	3	0.94–1.27	1.15	3	100.0	3	0.92–1.24	1.08	3	100.0
Σ	14	1,240–3,400	2,052	68–93	81.7	14	0.21–1.61	0.96	13	92.8	5	0.49–1.24	0.93	4	80.0

the fillets and fish weight for the 127 females (Figure 2). The weight of individual fish was evenly distributed in each of the area samples with the exception of the small sample of eight fish from Seattle. Although these were the largest fish collected, they contained less mercury than smaller fish from other areas. The Seattle sample does not appear to be adequate in number and may not be representative of the population. In all areas, except Seattle, the correlation coefficients were significant for the relationship of mercury content to weight (Table 2). The correlations between mercury content and fish length were significant but slightly lower in four of the five groups showing

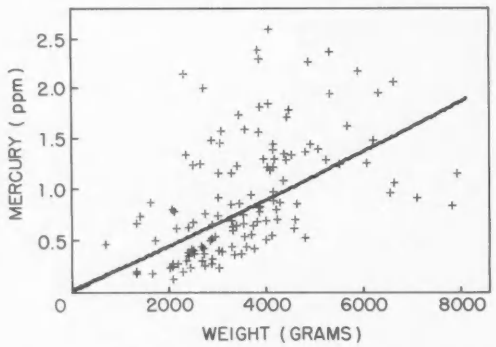

FIGURE 2.—Relationship between weight and mercury concentration in female dogfish fillets.

TABLE 2.—Correlation coefficients (r) and significance level (α) of mercury content to the weight and length of female spiny dogfish fillets from the State of Washington.

Location	No. of fish	Weight vs. mercury		Length vs. mercury	
		r	α	r	α
Port Townsend	22	0.645	0.01	0.507	0.05
Seabeck	12	0.648	0.05	0.616	0.05
Blaine	20	0.768	0.001	0.756	0.001
Port Susan	32	0.699	0.001	0.643	0.001
Seattle	8	−0.501	NS[1]	−0.414	NS
Tacoma	33	0.601	0.001	0.648	0.001
Σ	127	0.576	0.001	0.530	0.001

[1]Not significant.

positive coefficients. We expected a more significant correlation with length, since the weight of the females varied as to whether or not they were pregnant and the length of gestation. Childs et al. (1973) stated that mercury is not concentrated in the fetuses in situ; therefore, the mercury level in the flesh of the female is presumably unaffected by pregnancy.

The bellyflaps of 107 female and 5 male dogfish were analyzed (Table 1). Bellyflaps of the fish from Seattle and 10 small females from Port Susan were not analyzed. The bellyflaps contained slightly less mercury than the corresponding fillets; however, the percentage exceeding the action level (73%) was not significantly different from that for fillets.

The limited data on mercury levels in male dogfish (Table 1) indicated that essentially all male dogfish over the minimum commercial size (81.3 cm) would exceed the FDA action level. Of the 14 males analyzed, 13 (93%) exceeded the action level. The mean weight of the males (2,052 g) was less than the mean weight of the females (3,608 g), yet the mean mercury level was higher (0.96 ppm for males and 0.92 ppm for females). This difference may be attributed to the fact that males are smaller than females of the same age (Jensen 1966). Our findings agree with those of Forrester et al. (1972) on the mercury levels in male and female spiny dogfish from inland waters of British Columbia.

A study by Childs and Gaffke (1973) included 88 dogfish taken off the Oregon coast and showed a similar correlation of mercury level to weight and length but a lower mean level of 0.602 ppm mercury in all muscle samples. This suggests that dogfish taken from the Pacific Ocean off the Oregon coast may contain less mercury than the population sampled in this study of the inland waters of Washington. Tagging studies by Kauffman (1955) and Holland (1957) indicated that offshore dogfish populations may be highly migratory. Jensen (1966) noted that the nature of the dogfish's seasonal migration in offshore coastal waters was not clearly understood. Alverson and Stansby (1963) stated that the dogfish within Puget Sound show less tendency to migrate and that Puget Sound stocks are apparently somewhat independent from the coastal and offshore stocks. They further stated that some movement of dogfish may occur between ocean areas and Puget Sound. The mercury levels found in our study are most probably those of a population indigenous to Puget Sound.

Acknowledgments

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LOCALIZED MASS MORTALITY OF RED SEA URCHIN, *STRONGYLOCENTROTUS FRANCISCANUS*, NEAR SANTA CRUZ, CALIFORNIA

Johnson (1971) reported on the occurrence of a mass mortality of red sea urchin, *Strongylocentrotus franciscanus* (Stimpson 1857) off Point Loma, San Diego, in the summer of 1970, and she detailed the symptoms of the diseased sea urchins. Large areas of the test, particularly of the interambulacra, were denuded of spines and epidermis. These denuded areas were chalky white with green blotches and often were bordered by a ring of swollen tissue. The test plates of the denuded area were layered and a middle "red-friable" layer with disorganized cellular structure replaced the normal plate tissue and ossicle. In some cases, lesions broke through the denuded tests and these apparently led to the animals' death. The internal organs appeared to be normal. Johnson (1971) was unable to determine the cause of these symptoms, but she suggested that a microorganism, perhaps a fungus, might be responsible.

The area affected in the 1970 mass mortality off Point Loma was limited to a few hectares (Johnson 1971). It was first noted in May 1970, when the center of the area was littered with dying sea urchins while the perimeter had fewer diseased animals with only small patches of denuded tests. The affected area did not spread, and by the middle of summer, many of the surviving urchins were regenerating spines. Diseased animals with partially denuded tests were difficult to find in November 1970.

We report here two other localized mass mortalities of *S. franciscanus* in central California, which seem to be similar to the one documented by Johnson (1971). One was found in 3–5 m of water off the southeast side of Año Nuevo Island (lat. 37°06′25″N, long. 122°19′30″W). It was first observed on 18 July 1976, and revisited on 31 July 1976. Diseased animals with drooping spines and partially denuded tests were found scattered among healthy-appearing individuals. They did not seem to be clumped or segregated, although most diseased animals were in the open while healthy-appearing animals tended to be under ledges or in crevices. Diseased animals did not hold onto the rocks as normal animals usually do, and they were picked up easily by divers. Empty tests of recently dead animals littered portions of the bottom. Red sea urchins were the only animals noted to be affected at the Año Nuevo Island site. Other areas of similar depth to the south and northwest of Año Nuevo Island supported numerous healthy-appearing red sea urchins and none with denuded tests.

The diseased animals collected from Año Nuevo Island were very similar to those described by Johnson (1971) (Figure 1). Portions of the test were denuded of spines while the remainder of the test was covered with normal-appearing spines. The affected test plates were layered with a thin greenish surface layer, a red-friable middle layer

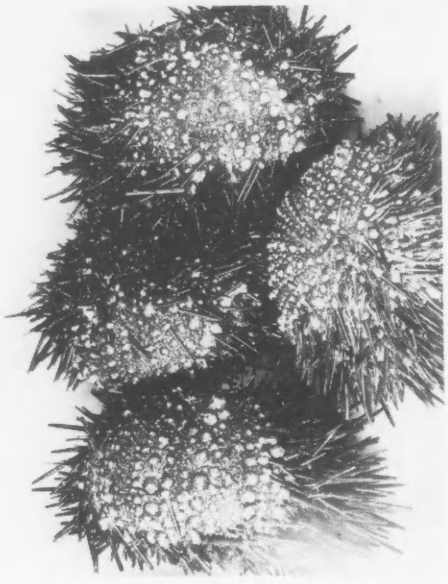

FIGURE 1.—Four diseased *Strongylocentrotus franciscanus* collected on 31 July 1976 from 3–5 m depth off Año Nuevo Island, Calif. Each animal is about 10 cm in diameter. Note the large portion of test denuded of spines in each animal.

and a nearly normal white inner layer (the "callus" layer, see Pearse and Pearse (1975) for description of the layers of the test plates and methods for examining them). Portions of the inner layer of the affected area were discolored reddish brown, however, often with a rather blotchy appearance. Clorox[1] cleaned and thin-ground preparations of the plates showed that middle layer of the diseased plates had lost much of its trabecular structure and there were large spaces between the middle layer and the inner layer. In the most diseased plates, the inner layer could be separated easily from the middle layer of the plates. The ambulacral system with the water vascular canals, ampullae, and radial nerve were all discolored reddish brown under the diseased portions of the test and much of these tissues were speckled with dark reddish-brown flakes, probably clumped coelomocytes. The internal organs in other portions of the diseased animals appeared normal.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

The symptoms noted in the diseased animals at Año Nuevo Island in 1976 seemed identical to those described for diseased animals found at Point Loma in 1970 by Johnson (1971). Such similarity suggests that the same disease organism may be involved in these mass mortalities. Alternatively, the symptoms could reflect a general response to localized infections or disruptions of the test from a variety of physical, chemical, or biological agents. As Johnson (1971) cautioned, careful microbiological work needs to be done before the causative agent(s) of these mass mortalities can be identified.

The Año Nuevo Island site of the mass mortality was revisited on 24 September 1976. Sea urchins were scarce compared with the earlier visit and most were nestled in crevices. Only one animal was found with symptoms of the disease; it had a narrow strip down one interambulacrum which was denuded of spines. However, when this animal was examined in the laboratory, it was found that a large portion of the diseased interambulacrum and adjacent ambulacrum was covered with short regenerating spines, and the ambulacrum was concave and grossly deformed. Six other normal-appearing animals were brought into the laboratory and two of these had small areas on the test with regenerating spines. From these observations, it appeared that the mass mortality had ceased and some of the animals survived and regenerated their lost spines.

The second mass mortality of *S. franciscanus* we found in 1976 occurred at 4–6 m depth off the east side of Point Santa Cruz (lat. 36°57′05″N, long. 122°01′30″W); this area was described by Mattison et al. (1977). Animals looking "sick" and losing spines were seen in the area in early June (A. L. Shanks, J. D. Trent pers. commun.). We did quantitative studies at fixed stations off Point Santa Cruz on 28–30 June 1976 and again on 10–11 September 1976. Although we found no animals with denuded tests at our study stations, there was a notable decrease in the number of animals present compared with the counts made in the previous two summers (Figure 2). The number of animals at the seaward edge of the kelp forest maintained densities of about 55–65/10 m² during the summers of 1974 and 1975. Fifty and one hundred meters seaward of the kelp forest, lower densities of 20–30 animals/10 m² occurred on the barren-appearing rocks. In the summer of 1976, we found only about 20 animals/10 m² at the edge of the kelp forest and about 1–2/10 m² 50 and 100 m

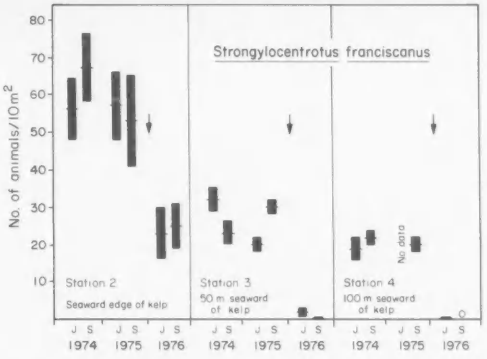

FIGURE 2.—Densities of *Strongylocentrotus franciscanus* at three fixed stations off Point Santa Cruz as estimated in June and September 1974, 1975, and 1976. Each station encompassed an area of 2,500 m² and the density estimates are based on counts from 12 randomly selected 10 m² quadrats. Station 1 was located 50 m inshore from Station 2 within the kelp forest and always contained very low densities of sea urchins, <1/10 m². Figure shows mean number of animals per 10 m² and the standard error of the mean. The arrows indicate the period of the mass mortality.

offshore. This represents a decrease of about 60% of the dense population of animals at the kelp forest edge and about 95% of the animals farther offshore. The area of each study station was about 2,500 m². In absolute terms, the decrease in number of animals within the study station at the edge of the kelp forest was about 9,000 animals, while in each of the two study stations 50 and 100 m farther offshore, about 5,500 animals were lost.

About 10% of the animals remaining in our Point Santa Cruz study site in June 1976 had large conspicuous portions of the test covered with regenerating spines only 1–5 mm long, contrasting noticeably with the surrounding normal-appearing areas. Since we did not detect any abnormalities in January 1976, the mass mortality probably followed its full course in less than 6 mo, as did the one described by Johnson (1971), and probably the one we observed at Año Nuevo Island.

During August–October 1976 we (M. B. Y. and C. R. A.) surveyed the 35-km coastline between Point Santa Cruz and Año Nuevo Island at 2-km intervals. Most of the kelp forests along this coastline have dense populations of *S. franciscanus* along their seaward edge, similar to conditions found at Point Santa Cruz before 1976. No evidence of mass mortality of these populations of sea urchins was found, either as large numbers of dying animals or unusually low numbers of animals. However, diseased animals with partially denuded tests were found occasionally all along the coastline with estimated incidences of 1 in 1,000 animals. These observations suggest that potential outbreaks of localized mass mortalities could occur in many places under suitable conditions.

The mass mortality of *S. fransicanus* at Point Loma in 1970 and those at Año Nuevo Island and Point Santa Cruz in 1976 were all relatively small and localized in both space and time. Moreover, all the animals in the populations were not killed. Rather, within less than 6 mo low numbers of normal and healthy-appearing animals were present and there was little trace of the mass mortalities—no piles of empty tests remained. Small localized mass mortalities might occur in other areas and not be noticed or reported. If they do, such mass mortalities could be important in regulating the distributions and densities of sea urchin populations. Moreover, since a major portion of the recruitment of juveniles of *S. franciscanus* occurs under adult animals (Tegner and Dayton 1977), near complete mass mortalities, such as that in our study stations 50 and 100 m seaward of the kelp forest off Point Santa Cruz, could have long lasting effects. Such a source of mortality could have practical importance both as means of minimizing overgrazing of kelp by sea urchins (North and Pearse 1971) and as a threat to the developing sea urchin fishery in California (Kato 1972).

Acknowledgments

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FIRST RECORD OF A SECOND MATING AND SPAWNING OF THE SPOT PRAWN, *PANDALUS PLATYCEROS*, IN CAPTIVITY

The spot prawn, *Pandalus platyceros* Brandt, is the largest species of the family Pandalidae. It supports a minor fishery within its range of San Diego to the Bering Strait, Korea, and Japan in depths to 532 m (Butler 1964). The prawn is being studied at the National Marine Fisheries Service (NMFS) Aquaculture Research Station, Manchester, Wash., as a possible companion crop to Pacific salmon reared in floating net pens (Mahnken 1975; Prentice 1975). One phase of this work is to investigate the reproductive potential of the prawn in captivity.

The prawn is a protandric hermaphrodite, i.e., an individual matures first as a male (at age 1.5 yr), breeds one or more times as a male, passes through a transitional phase (at age 2.5 yr), and becomes a functional female (at age 3.5 yr) (Butler 1964). In studies of natural populations in southern British Columbia, Butler (1964) found that few if any females breed more than once and suggested that the females die soon after spawning.

At the Aquaculture Research Station, prawn culture and breeding experiments have been carried out since 1973. The matings reported in this study were made with laboratory-cultured males and captured, wild females. The females were captured in ovigerous condition in 1974 from Hood Canal, Wash., and their eggs hatched in the laboratory during February and March 1975. Therefore, we know these females have spawned at least once, and since their prior history is unknown, there is the possibility that some or all may have spawned more than once.

The spawned females (103) were held from March to August at the Aquaculture Research Station in floating net pens or in benthic cages 10 m beneath floating net pens containing salmon. The postspawning survival was 100% through August 1975 for both groups. All prawns in the net pens were maintained on a diet of frozen clam meat, *Panope generosa*, and salmon mortalities. The benthic cage group did not receive any supplemental food.

In August varying densities of spawned females and cultured males (Table 1) were placed either in three net pens, eight laboratory tanks, or in a benthic cage. The net pens were constructed of 18-mm mesh (stretch measure) knotless nylon with 6.8 m^2 of substrate per pen available to the prawns. The top of each pen was covered with black plastic sheeting. Each laboratory tank had 0.24 m^2 of available substrate. All water entering the tanks was sand filtered and not recycled. The single benthic cage was constructed of vinyl-coated wire mesh (9.0-mm stretched measure) and had 2.6 m^2 of substrate available to the prawns. All test groups were fed the clam–salmon diet with the exception of those in the benthic cage which received no supplemental food. A continuous low-level mortality was observed among the females from August to early October 1975 which reduced their survival to 39.8%.

Survival of the female prawns was not dependent upon stocking density; however, survival was significantly greater in the benthic cage and laboratory tanks than in the net pens (Table 1).

TABLE 1.—Survival (percent in parentheses) and second spawning of female *Pandalus platyceros* in three seawater systems.

Container type	No. of prawns per container		Density of prawns[1]	Survival of previously spawned females	Survivors spawning a second time
	Female	Male			
Benthic cage (9 m deep)	5	5	3.8	4 (80.0)	3 (75.0)
Net pen 1	29	56	12.5	12 (44.8)	10 (84.6)
Net pen 2	24	43	9.9	6 (25.0)	4 (66.7)
Net pen 3	29	89	17.4	6 (20.7)	5 (83.3)
Laboratory tanks[2]	2	2	16.7	12 (75.0)	12 (100.0)

[1]Prawns per square meter of available substrate.
[2]A total of eight laboratory tanks.

Females held in the bottom cage or in the laboratory tanks were subject to less ambient light, more stable temperatures, and water below the photosynthetic zone. The laboratory water system utilizes water pumped from an area 2 m above the sea floor, thereby approximating the water available to the bottom caged prawns. Previous work has shown that juvenile and yearling prawns are sensitive to rapidly fluctuating water temperature, light, and plankton blooms (Rensel and Prentice[1]).

A second spawning was recorded for 85.4% of the surviving females. The average carapace length of these spawners was 39.2 mm (SD = 1.31). Eggs developed normally, producing viable larvae, but the fecundity was low, ranging from 10 to 1,000 eggs. The fecundity of wild bred stocks is 2,000–5,000 eggs per female. The reduced fecundity in the female prawns spawning for the second time may be due to nutritional or environmental factors. However, in some instances the female prawns were observed actively removing eggs from their own abdomens, using the second pereiopod. In other cases, we observed egg losses during the holding period due to abrasion on the nets and tanks.

Multiple breeding and spawning are common in other families of caridean shrimps, but among the Pandalidae only *P. montagui* Leach in the northeastern Atlantic Ocean has been known to spawn for two consecutive years (Allen 1963). This study shows that female spot prawns can also successfully breed, spawn, and hatch eggs for a second time. This is important to both the aquaculturist and the field biologist. If multiple breeding also takes place in wild populations, then estimates of year-class recruitment based on single spawning populations are in error.

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EFFECT OF DISSOLVED OXYGEN CONCENTRATION AND SALINITY ON SWIMMING SPEED OF TWO SPECIES OF TUNAS

Studies on captive skipjack tuna, *Katsuwonus pelamis*, have determined three physiological parameters that may operate to delimit oceanic distribution of this fish. If 1) a lower temperature limit of 18°C, 2) a size-dependent upper temperature limit, and 3) a lower oxygen limit of 5 ppm are mapped onto the temperature and oxygen levels of the central Pacific area, the resulting model is consistent with many of the peculiar features of the geographical distribution of the skipjack tuna (Barkley et al.[1]). In particular, the exclusion of adult skipjack tuna from warm, oxygen-poor waters of the eastern tropical Pacific Ocean is explained.

But the physiological parameters used in the model were either speculative—upper temperature limits—or based upon acute and stressful experimental conditions—lower oxygen and temperature limits. Gooding and Neill[2] determined the lower oxygen limit by introducing tunas into a small tank (1.8 × 2.4 × 0.6 m oval) containing

[1]Barkley, R. A., W. H. Neill, and R. M. Gooding. Skipjack tuna habitat based on temperature and oxygen requirements. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.–1 Oct. 1975.)

[2]Gooding, R. M., and W. H. Neill. Respiration rates and reactions to low oxygen concentrations in skipjack tuna, *Katsuwonus pelamis*. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812.

seawater at a given level of oxygen saturation. Swimming speed and survival time were measured. They found that survival time and swimming speed were independent of oxygen levels in excess of 4 ppm; below 4 ppm survival time was directly and swimming speed inversely proportional to dissolved oxygen amounts. So apparently 4 ppm is close to the incipient lower lethal limit for skipjack tuna under the given experimental conditions. For modeling distribution limits, Barkley et al. (see footnote 1) used a more conservative figure of 5 ppm.

However, a physiological limit of 4 or 5 ppm is not necessarily a behavioral limit; if the limit is approached slowly under natural and otherwise unstressful conditions, can a fish adaptively respond? Whitmore et al. (1960) found that coho salmon, *Oncorhynchus kisutch*, avoided water of lowered oxygen levels yet which produced no respiratory distress. In contrast, kawakawa, *Euthynnus affinis*, a species closely related to skipjack tuna, tolerated 2-ppm water for short periods in order to get food (Chang and Dizon[3]).

In the present experiment, I tested the responses of free-swimming tunas—both skipjack tuna and yellowfin tuna, *Thunnus albacares*—encountering slowly changing oxygen levels. The rate of change was comparable with that which a tuna might encounter in nature. Yellowfin tuna were tested for comparison because they are abundant in the same areas of the eastern tropical Pacific avoided by large skipjack tuna. Finally, salinity fronts have been suggested as a factor determining distribution, so responses to decreasing salinity levels were also examined.

Materials and Methods

Eight skipjack tuna and three yellowfin tuna were tested with decreasing oxygen levels, and three skipjack tuna, and one yellowfin tuna were tested with decreasing salinity levels. Fish were chosen from stocks at the Kewalo Research Facility of the Southwest Fisheries Center, National Marine Fisheries Service, NOAA, Honolulu, Hawaii. Tuna stocks for this experiment were kept in outdoor tanks (7.3 m diameter × 1.2 m deep) until used; they were then removed by angling with a barbless hook and transferred to the swim chamber in a plastic bag partially filled with water. This is a good transfer technique since fish on occasion have fed immediately after transfer.

The responses of tunas to decreasing oxygen and salinity levels were examined in a tank system consisting of a swim chamber equipped with photocells for monitoring and recording fish behavior. (For details see Dizon et al. 1977.) The swim chamber was a 6.1 m diameter × 0.61 m deep fiber glass tank fitted with a concentric inner wall so the fish was constrained to swim in a 0.75-m channel around the periphery. Six laps equaled 100 m. Water (24°C) was introduced and removed from the swim channel through two pairs of concentric rings of polyvinyl chloride pipe. Entering (or exiting) water divided equally into two inflow (or outflow) pipes, each flowing countercurrent to the other to provide minimum oxygen or salinity asymmetry and horizontal transport of water within the swim channel. Water was recirculated through an outside circuit at 1,136 liters/min to insure thorough mixing of any introduced new water. New seawater was added to the tank at 38 liters/min.

Oxygen was reduced in the tank by replacing the 38 liters/min new seawater with 38 liters/min anoxic seawater obtained at our well head before aeration and introduced into the intake of the 1,136 liters/min recirculation pump. Oxygen decreased approximately exponentially within the swim chamber—0.06 ppm/min after 30 min and 0.03 ppm/min after 60 min. Salinity levels in the swim chamber were reduced by introducing aerated freshwater (38 liters/min) into the pump intake. Salinity decreased exponentially—0.07‰/min after 30 min and 0.03‰/min after 60 min.

Passage of the fish was sensed at four photocell stations (six photocells/station) at 90° intervals around the periphery of the swim channel. Information from the photocells was translated into swimming speed (minutes per lap), direction (clockwise or counterclockwise), and frequency of reversals or swimming direction by digital logic equipment and printed on adding machine tape.

Procedures were quite simple; tuna (starved for 1 day) were moved into the tank and allowed 100 min to habituate; swimming speeds were continuously recorded to provide baseline data to compare with behavior during periods of changing oxygen or salinity. After 100 min, a test was started and behavior was recorded as salinity or oxygen decreased. Oxygen and salinity levels were allowed

[3]Chang, R. K. C., and A. E. Dizon. Low oxygen levels as barriers to voluntary movements of tunas. Manusc. in prep. Southwest Fish. Cent. Honolulu Lab., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96812. (Material presented at 26th Tuna Conference, Lake Arrowhead, Calif., 29 Sept.–1 Oct. 1975.)

to reach 2 ppm and 29‰, respectively. After reaching these levels (about 200 min), test water was shut down and normal seawater restored. The following morning fish were removed, weighed, and measured, and survivors were returned to holding tanks. Oxygen and salinity levels were monitored by oxygen meter and salinograph; samples were taken periodically for laboratory analysis to verify the instruments.

Results and Discussion

Behavioral responses to decreasing levels of salinity were unremarkable; Table 1 summarizes results from three skipjack tuna and one yellowfin tuna. No consistent swimming speed changes were observed during periods when salinity decreased from about 34‰ to 29‰. Although sample size is small, these tunas did not make any dramatic response to salinity changes of magnitudes expected within their normal habitat.

Figure 1 illustrates typical results from tunas encountering slowly changing oxygen concentration. At or about 4 ppm, skipjack tuna (Figure 1a) demonstrated an abrupt increase in swimming speed. In most fish tested, speed increased to over 2 lengths/s. Yellowfin tuna, in contrast, showed no alteration in swimming speed as oxygen levels decreased (Figure 1b).

Figure 2 summarizes the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Individual points plotted are median swimming speeds for the eight skipjack tuna grouped by: 1) before treatment and 2) 1-ppm dissolved oxygen intervals both decreasing and increasing, i.e., 6–5, 5–4, 4–3, 3–2, and 2–3, 3–4, 4–5, 5–6. Number of swimming speeds sampled ranged from under 5 to over 100 depending on the number of laps swum during each interval. Heavy line connects the grand median of each interval. Similar data for each yellowfin tuna (decreasing oxygen intervals only) are included for comparison.

TABLE 1.—Effect of decreasing salinity on mean swimming speed in tunas.

Item	n	$\bar{X}$ (length/s)	SD
Skipjack tuna 1 (38.3 cm, 925 g)			
Before salinity change	28	2.10	0.40
During salinity change	22	1.82	0.40
Skipjack tuna 2 (37.7 cm, 882 g)			
Before salinity change	44	2.03	0.26
During salinity change	12	2.37	0.19
Skipjack tuna 3 (42.0 cm, 1,352 g)			
Before salinity change	30	1.21	0.07
During salinity change	15	1.16	0.06
Yellowfin tuna 1 (45.3 cm, 1,491 g)			
Before salinity change	39	1.54	0.30
During salinity change	31	1.81	0.26

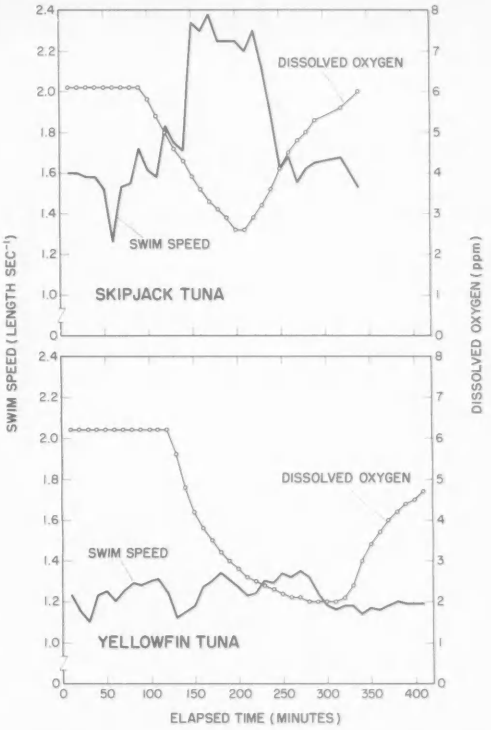

FIGURE 1.—Effect of dissolved oxygen level on swim speed in two species of tunas. Swim speeds are median values sampled for 10-min periods.

Not all of the skipjack tuna survived the treatment; three of the eight died when oxygen levels dropped below about 2.5 ppm. Survival times for skipjack tuna under conditions of low oxygen are as follows: in excess of 240 min at 4 ppm, 59 min at 3 ppm, and 18 min at 2 ppm (Gooding and Neill see footnote 2). My data are consistent with this resistance–time distribution, and both studies support the Barkley et al. (see footnote 1) hypothesis that there does exist a low oxygen level that limits the observed oceanic distribution of skipjack tuna.

Yellowfin tuna are not apparently stressed during the exposures to the low oxygen water employed. In separate tests done after the exposures to decreasing oxygen, two additional yellowfin tuna survived and made no overt locomotory changes when introduced directly into water

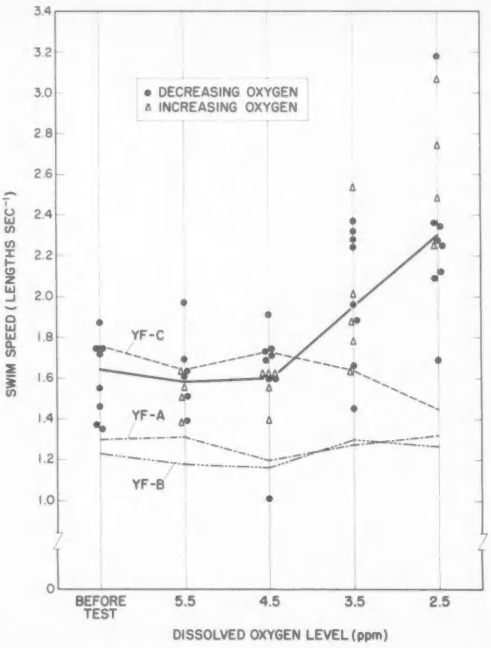

FIGURE 2.—Summary of data from the oxygen experiment observations from eight skipjack tuna and three yellowfin tuna. Dots — decreasing oxygen levels, median swim speeds grouped by 1-ppm intervals and "before" test observations. Open triangles — increasing oxygen levels, median swim speeds grouped by 1-ppm intervals. Solid line — grand median for eight skipjack tuna. Broken lines — medians for each of the three yellowfin tuna, decreasing oxygen levels only.

containing 1.4 and 1.6 ppm oxygen. They survived a 200-min exposure and a 100-min recovery period. By way of contrast, brook trout, *Salvelinus fontinalis*, LD_{50}'s for 1.5 ppm and 1.4 ppm were 300 and 100 min, respectively (Shepard 1955). The brook trout and the yellowfin tuna were swimming at about the same speeds, 1.0–1.5 lengths/s. Although conditions of the two experiments are in no way similar, these data do imply that yellowfin tuna are at least as low oxygen tolerant as brook trout. The higher energy requirements (larger fish, warmer water) of yellowfin tuna allow this conclusion. Perhaps if oxygen levels dropped low enough in my tank (1.4 ppm is about the lowest that could be achieved), an increase in speed similar to that in skipjack tuna would have been observed.

Increased swimming speed should function either to remove the fish from suboptimal areas (if coupled with some directive stimuli) or to provide more water to the gills—tunas are ram ventilators. Within the skipjack tuna habitat, water deficient in oxygen is found within and below the thermocline (Barkley et al. see footnote 1). Appropriate behavior would be to swim up and out of the low-oxygen water. Even without a change in direction, angle of attack of pectoral fins, or body attitude, increased swimming speed alone will cause a tuna to rise due to increased lift (Magnuson 1973).

Faster swimming speeds do not seem to be a response to increase ram ventilation (open mouth swimming). Increased flow over the gills providing more oxygen delivery is offset by increased respiratory demands imposed by faster swimming. Under conditions of saturated seawater (7.2 mg O_2/liter), 15% head loss along the respiratory flow path (Brown and Muir 1970), a conservative oxygen utilization factor of 75% (Stevens 1972), and a 1 cm^2 mouth gape (Brown and Muir 1970), oxygen is delivered to the gills at the rate represented by the middle broken line (Figure 3). This, of course, also increases as swimming speed increases. Respiratory demand (solid black line) and oxygen delivery intersect at two points: the lower is at the minimum swimming speed that can still furnish sufficient oxygen for an animal in an almost basal state and the upper is a point at which exponentially increasing respiratory demand again exceeds linearly increasing oxygen delivery.

The latter would seem to be maximum sustained swimming speed; anaerobic metabolism would be necessary at speeds above. However, neither function (anaerobic or aerobic) may be correctly extrapolated to the faster swimming speeds. Respiratory demand might well be less at higher speeds if swimming efficiency increases.

Yet, if dissolved oxygen concentration drops to 4 ppm, increase in swimming speed is an inefficient way to make up the deficit (lower broken line). But, increase gape to 2 cm^2 (I am assuming for argument's sake that this doubles ventilation volume) restores the amount of oxygen delivered (upper broken line). In summary, I suspect that increased swimming speed of skipjack tuna encountering oxygen-deficient water is not due to ram ventilation needs but rather is a behavioral response to remove an animal from a suboptimal area. Considering the relative expense of faster swimming in terms of oxygen needs, the modest increases in swimming speeds observed are probably very adaptive in that they should cause a

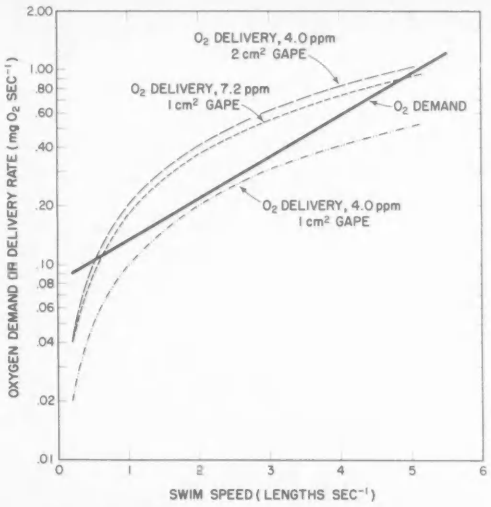

FIGURE 3.—Respiratory demand (Gooding and Neill see footnote 2) versus respiratory supply (Brown and Muir 1970; Stevens 1972) as a function of swimming speed in a 40-cm, 1.4-kg skipjack tuna. Respiratory demand increases geometrically while respiratory supply increases arithmetically with increasing swimming speed. When oxygen concentration decreases it is more efficient to increase ram ventilation by increasing gape rather than simply swimming faster.

fairly rapid rise in the water column at a relatively low energetic cost. Yellowfin tuna, in contrast, are just not stressed at the levels of saturation employed in our experiments. Yellowfin tuna should be able to occur in the anoxic water in or below the thermocline and since in the eastern central Pacific Ocean anoxic, cool waters are as inhospitable as the upper too warm waters, skipjack tuna may find no suitable habitat.

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A NONLETHAL LAVAGE DEVICE FOR SAMPLING STOMACH CONTENTS OF SMALL MARINE MAMMALS

Historically, the only expedient and successful method for determining the species upon which marine mammals feed has been to kill the animal, remove its stomach, and examine the contents in the laboratory (e.g., Wilke and Nicholson 1958; Tautsumi et al. 1961; Shomura and Hida 1965; Fiscus and Baines 1966; Fitch and Brownell 1968; Imler and Sarber 1947). This method, however, does not always work. For example, when actively feeding marine mammals are harpooned or shot, they sometimes regurgitate most or all of their food. While regurgitation by live captured marine mammals is possible, it does not appear to be a significant problem. Of the last 10 cetaceans that I have captured alive and later released unharmed, none has regurgitated during the capturing, handling, or releasing process. Although some researchers have reported on stomach samples from stranded marine mammals (e.g., Houck 1961; Fitch and Brownell 1968), these samples may not be representative of feeding habits of active healthy organisms.

Passage of the Marine Mammal Act in 1972 has made it necessary to develop techniques beside killing if we are to continue certain types of marine mammal research. A useful tool for determining feeding habits of delphinids and certain small pinnipeds would be a portable stomach pump device capable of being used in the field. To be effective, this device must be capable of removing small identifiable bits of food such as otoliths, scales, preopercular bones, squid beaks, or other

skeletal elements from the stomach of a pinniped, or forestomach of a small cetacean. I do not consider it essential to be able to remove whole fish or squid from marine mammal stomachs, as several recent or current marine mammal food habit studies have successfully utilized the above-mentioned skeletal elements for prey species identification (Fitch and Brownell 1968; Evans 1975; Burns and Lowry 1976).

Soft tissue digestion in pinnipeds and small cetaceans is normally quite rapid, thus it is possible to remove partially digested skeletal elements from the stomachs of live animals a few hours after the animal has eaten; and yet, because such elements as otoliths, preopercular bones, and squid beaks tend to resist this rapid digestion, they are still available for removal several hours after being consumed. In this paper I report on development and testing of a lavage designed to sample marine mammal stomach contents without killing the animal.

Methods

Several design criteria were considered essential. The lavage unit had to be effective in removing skeletal elements, simple to operate, portable, and capable of being used without injuring the animal. Discussions with persons who had pumped human stomachs or were familiar with the characteristics of marine mammal digestive tract anatomy resulted in the decision to utilize a water-driven aspirator to create suction. A 30-mm outside diameter by 1.0-m long Rousch Equine[1] endotracheal tube was modified for use as the irrigation and content removal device. These two pieces were coupled to a machined Plexiglas stomach content collection chamber with short sections of clear vinyl tubing. A ball valve was attached to the aspirator for vacuum control. The completed unit utilized normal city water pressure (35–50 psi) delivered through a 12-mm diameter rubber hose to the ball valve as driving source for the aspirator. A small hand pump was connected to the irrigation port on the side of the entubation tube so that warm (25°–35°C) water could be pumped into the animal's stomach to create a slurry which could be easily removed by light suction. To facilitate removal of this slurry, the entubation tube was modified by sealing the distal end (stomach end) with a machined Nylon plug, opening a side suction port (8.9 cm long by 1.25 cm wide) in the side of the tube 5 cm back from the Nylon plug, and removing the inflation cuff to allow passage of the irrigating solution into the stomach opposite the suction port. The assembled unit is detailed in Figures 1 and 2. The completed unit was tested in the laboratory using a 2-liter beaker in place of a marine mammal stomach.

Marine mammals were first tested at the Naval Undersea Center and Sea World, Inc. in San Diego, Calif., in December 1975. A total of five animals were lavaged, including two California sea lions, *Zalophus californianus*, two Pacific white sided porpoise, *Langenorhynchus obliquidens*, and one bottlenose porpoise, *Tursiops truncatus*. Animal weights ranged from 70 kg for the smallest *Z. californianus* to 210 kg for the *T. truncatus*. All animals except a 100-kg *Z. californianus* had fasted for at least 24 h prior to being lavaged. The

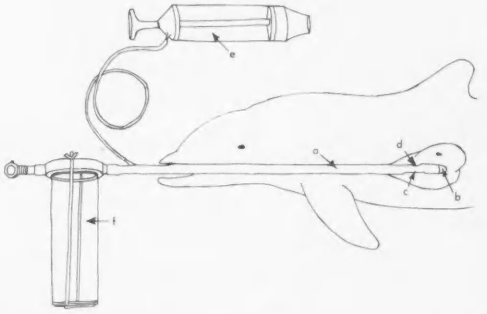

FIGURE 1.—Schematic of lavage device. Entubation tube (a), Nylon end plug (b), side suction port (c), irrigation port (d), irrigating solution hand pump (e), stomach content collection chamber (f).

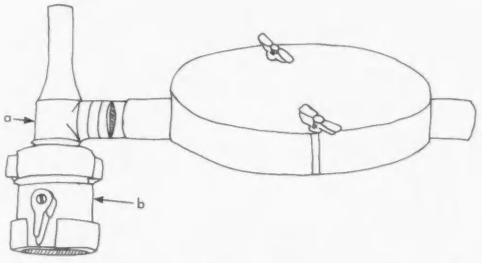

FIGURE 2.—Oblique view of the aspirator (a) and control valve (b) attached to the top of the collecting chamber of lavage device.

[1]Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

100-kg sea lion had been fed 5 kg of surf smelt, *Hypomesus pretiosus*, 3 h prior to being lavaged.

Successful lavage required two procedures: 1) restraint of the animal and 2) entubation, irrigation, and suction. Restraint varied greatly depending on whether a pinniped or cetacean was to be lavaged. Delphinids are generally easy to restrain. The procedure many investigators have used with success utilizes a canvas sling and U-shaped pipe frame to hold the animal (Ridgway 1972). Normally the use of a sling is sufficient restraint, however A. B. Irvine (pers. commun.) has also used a wooden step ladder covered with closed cell foam padding and padded straps to restrain large or especially aggressive delphinids. This latter procedure requires that the animal be gently lowered onto the padded ladder and then immobilized with the padded straps. Pinnipeds are more difficult to restrain in the field than delphinids. Squeeze cages (Ridgway 1972) are generally effective, but are normally too cumbersome and heavy to use at sea. During the lavage test in San Diego, the squeeze cage was used with success, though considerable care was taken to avoid being severely bitten. Use of the padded wooden ladder and straps as a restraining technique for pinnipeds in the field appears reasonable but needs testing.

With the animal successfully restrained, we proceeded with entubation after lubricating the entubation tube with a jelly lubricant. The plugged end of the tube was gently pushed down the animal's esophagus. After completing the entubation I waited a few moments to make sure the animal was breathing normally. If the animal gagged or abnormal respiration was evident, I quickly but gently removed the tube. If respiration was normal, I connected the content collection chamber and irrigation solution hose and pumped about 300 ml of warm water into the stomach. Warm water was used to avoid thermal shock to the stomach. I then opened the vacuum control valve and applied suction to the stomach. As suction began to remove the stomach content slurry, more irrigating solution was pumped into the stomach. In this manner a 2- to 3-liter food sample was collected in a period of about 5 min. When I felt I had collected sufficient material for test purposes, I shut off the suction, ceased pumping irrigating solution, and gently removed the stomach tube. The stomach contents were filtered from the slurry using a small hand vacuum pump and then preserved in 70% alcohol.

Results

Using the above procedure otoliths, muscle myomeres, skeletal bones, and scales were collected from all five marine mammals. The animals tested were returned to their tanks unharmed and were doing well several days later.

Discussion

Using the equipment described and associated procedure it was possible to remove almost all of the diluted stomach slurry by suction; and by rotating the tube while suctioning, it was possible to vacuum the rugae of the stomach in order to collect otoliths and squid beaks which tend to accumulate in these folds. J. E. Fitch of the California Department of Fish and Game has used fish otoliths as a means to identify prey species on a routine basis. With experience it is possible to correlate size of otoliths and approximate sizes and weights of the intact fish. The Alaska Department of Fish and Game is presently establishing such an otolith reference collection, allowing not only identification of otoliths but also estimation of intact prey length and weight (L. F. Lowry pers. commun.).

The limiting factor in the use of this device appears to be the ability of the capture personnel to restrain specimens. Pinnipeds over 150 kg are probably too large to be effectively restrained mechanically, and are therefore very difficult or impossible to entubate. Cetaceans, perhaps as large as 500 kg, can be effectively entubated and lavaged since these animals are generally much more easily restrained out of water than the pinnipedia. In addition, certain pinnipeds, e.g., *Erignathus barbatus*, *Phoca hispida*, *P. fasciata*, feed to a greater or lesser degree on soft-bodied crustaceans, and these prey organisms would probably be effectively destroyed by suction and passage through the entubation tube (L. F. Lowry pers. commun.).

I have made no mention of the use of chemorestraining techniques because I feel that these methods are still unsuited for general use in the field, especially with cetaceans. With proper supervision, they have proven effective for restraining captive pinnipeds. In August 1972, I used a chemorestraining solution of Ketamine–Atropine on *Z. californianus* in the field. Although dosages were at the level recommended by marine mammal research veterinarians, I found the drugs

to be too slow acting to be generally effective for stopping highly mobile pinniped species before they could reach the sea. Two major drawbacks to chemorestraints in a field situation are judging animals' size adequately for effective dose determination, and the time required for the animal to recover sufficiently to be able to swim unassisted and maintain pace with the herd or pod from which it was captured. Should future work develop either drugs or techniques which allow safe and semi-instantaneous chemorestraint of any marine mammal species, then these drugs or techniques would be extremely useful when used in connection with the stomach pump. Until such drugs are available, I believe physical restraint is indicated during the lavage procedure.

Acknowledgments

I am indebted to S. H. Ridgway and the personnel at the Naval Undersea Center for their patience and cooperation, and to Lanny Cornell and his staff at Sea World, Inc. for their cooperation during testing of this lavage device. I thank L. F. Lowry of the Alaska Department of Fish and Game and A. B. Irvine of the U.S. Fish and Wildlife Service for their comments concerning restraint and use of this technique. I also thank Larry Hobbs and Mike Honing of University of California Santa Cruz and Steve Leatherwood of the Naval Undersea Center for assisting me during tests of the lavage. Thanks also to S. B. Stone of Marine General Hospital, K. S. Norris, T. P. Dohl, and R. W. Pierce of University of California Santa Cruz for their comments concerning design of the equipment. K. S. Norris, J. S. Leatherwood, W. E. Evans, T. P. Dohl, and Robert Hoffman reviewed the manuscript. This work was supported by contract number MM4AC013 from the U.S. Marine Mammal Commission.

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